Flight-morphology of Central European caddisflies (Insecta: Trichoptera) in relation to their ecological preferences

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Abbreviations

AR I **Aspect ratio I** is a dimensionless measure wing shape and is calculated by dividing wing length by wing width of the fore and hind wings combined, as the fore and hind wings of caddisflies operate in flight as a single lifting surface (Grodnitsky, 1999)

AR II **Aspect ratio II** is defined as the ratio of the wing span to its mean chord; therefore, it is calculated as wing span squared divided by total wing area and is a dimensionless number (Lindhe Norberg, 2002).

PC1 **Principal Components axis 1** is the first axis identified by the Principal Components Analysis.

PC2 **Principal Components axis 2** is the second axis identified by the Principal Components Analysis.

RTM **Relative thorax mass** gives the proportion of total mass to thorax mass.

RWA **Relative wing area** is the ratio of the forewing length to the total wing area of one species; it gives information on the relation of the individual to its wing area.

RWL **Relative wing length** is the ratio of forewing to body length (Malmqvist, 2000).

Background

The topic of adult dispersal in Trichoptera has been discussed for a long time (Nishimura, 1967; Crichton, 1971; Svensson, 1974; Coutant ,1982; Jackson & Resh, 1989; Sode & Wiberg-Larsen, 1993; Winterbourn et al., 2007). This topic lately reappeared as European legislation demands a "good ecological status" of freshwater habitats by 2015. This fuelled the restoration-process of many European freshwater ecosystems during the last decade. The success of such restorations is measured by the ecological status of the habitat. Once the physical environment is established, the (re-)colonisation of newly restored or built habitats can start. The presence of caddisfly larvae and relative abundance are used in the biological assessment and monitoring of water quality (Holzenthal et al., 2007). Hence, we started a medium scale morphometrical investigation on flight morphology of central European Trichoptera.

The order Trichoptera is among the most important and diverse of all aquatic taxa, and contains 600 genera, and approximately 13,000 species worldwide (Holzenthal et al., 2007). More than 1000 species are described for Europe (Malicky, 2005). Additionally, this widely distributed, amphibiotic insect group constitutes an important fraction of biomass in most running water ecosystems (Illies, 1958; Waringer, 1986).

Caddisfly species prefer lentic or lotic current regimes as they have evolved into a highly diverse fauna that exploits nearly all habitats from high altitude trickles to lowland rivers, wetland, standing water bodies, hygropetric habitats with some species even living in moist areas along springs and streams or in brackish water (Graf et al., 2008). In aquatic food webs larvae are vital participants. While some species tolerate a wide range of ecological conditions, others are much more specific (Graf & Schmidt-Kloiber, 2008). Running water bodies undergo longitudinal changes and the occurrence of species changes in it. The composition and structure of stream biotic communities have been shown to change in response to longitudinal changes in habitat characteristics, such as temperature, current velocity, depth, width, discharge, substratum, turbidity and food availability (Hynes, 1970; Fisher, 1982; Allan, 1996).

The egg, larval and pupal stages are mainly aquatic, while the adults live in the terrestrial environment (Graf & Schmidt-Kloiber, 2008). The adults are generally considered strong fliers because most species are fully winged, and many of them display intricate swarming flights (Johnson, 1969; Gullefors & Petersson, 1993). The primary purpose of the adult phase of the

typical aquatic insect life cycle is mating and the deposition of eggs in habitats suitable for larval development (Kovats et al., 1996). We find broad variation of life cycle styles such as longevity or emphemerallity, habitat generality or specialism, dispersing males or females, and feeding or non-feeding imagos. In some species the terrestrial phase is quite short and it is the only opportunity to disperse. Individuals disperse either actively by flight or passively by wind drift. Most of the time it will be a combination of both movements as the distance between catchments varies. The occupation of new habitats is necessary to ensure the survival of populations through gene transfer. The structure of the gene transfer is defined by the dispersing sex and fecundity state. Ross (1944) stated that some teneral (immature adult) caddisflies move inland, where they may rest until they become sexually mature. Dispersing males and immature females enrich the gene pool of an existing unrelated population, but gravid females have the potential to re-colonise new habitats. The important parameter for these exchange- and colonisation-processes is the range of one dispersing individual which is species-, maybe sex-specific. Some studies prove males as the dispersing sex in *A. fuscipes*, *L. reducta* and *S. pallipes* (Sode & Wiberg-Larsen, 1993), while Kovats et al. (1996) found female-biased sex ratios which support the idea of the dispersing females. Already Svensson (1974) stated that the sex-ratio may be associated with species-specific developmental or reproductive behaviour. If dispersal is considered as gene transfer males can be considered as the distributing sex as well.

The velocity of the colonisation of a new habitat depends on various circumstances. Rapid (re-)colonisation will occur in catchments where the species is already present (e.g. Müller, 1982). If the species does not occur in a catchment (re-)colonisation will be slower and will require the immigration of gravid females from elsewhere. The (re-)colonisation potential of a species will depend on species-specific factors such as behaviour, flight strength and dispersal, physical factors such as the distance between the streams and/or catchments, and the weather (Sode & Wiberg-Larsen, 1993). Unfortunately, information upon flight range values in Trichoptera in literature is scarce and contradicting observations are documented. Distances recorded varied from a few dozen meters perpendicular to a river (Sode & Wiber-Larsen 1993), to upstream flight distance of several kilometres for different Hydropsychidae (Coutant, 1982), and to multi-directional flight ranges of several dozens of kilometres and vertical migration in different *Limnephilus*-species (Malicky, 1987). Considerable variation in dispersal tendencies among species and sexes were also revealed by several population genetic studies (e.g.

Waringer, 1989; Bunn & Hughes, 1997; Hughes et al., 1998; Wilcocket al., 2001; Kelly et al, 2002). Another aspect is the timespan available for dispersal. Low dispersal may also be a consequence of the short lifespan of some adult Trichoptera (Sode & Wiberg-Larsen, 1993).

Yet another aspect is the larval habitat requirements which demand different dispersal abilities. Dispersal strategies are adapted to such different habitats like lentic or lotic water bodies. Lentic macroinvertebrates occur in isolated, island-like habitats, separated by inhospitable terrestrial landscape (Van de Meutter et al., 2006) and dispersal between lentic habitats may be achieved by active flight or passive dispersal over land (Bilton et al., 2001). On average, if evolutional time frames are considered, lotic habitats are more stable and predictable over space and time than lentic habitats (Marten, Brändle & Brandl, 2006) and therefore, lentic habitats should be favourably inhabitated by species with higher dispersal capacities which would ensure population survival of lentic species and should be significantly higher than in lotic species.

The necessity to bypass hostile habitats (terrestrial environment) is enabled by aerial transport. The distance travelled by air consists of two different movements: first, there is the active flight of the individual, and second, there is passive wind drift. These movements contribute to the distance travelled by one individual. Morphologically determined is the process of distance travelled actively.

Flight is enabled through wings and flight muscles, which represent the basic flight-morphologic equipment. Wainright (1994) stated that morphology and function are often associated. Consequently, morphology may therefore provide a useful indication of dispersal ability (Hoffsten, 2004). Some of these morphological factors are wing length, total wing area, as well as size-independent indices like RWL (RWL), and variously calculated ARs of the wings (Vogel, 1981; Malmqvist, 2000; Lindhe Norberg, 2002). However, empirical evidence linking morphology, dispersal ability, and distribution in aquatic insects is rare, except some studies on wing morphology in water striders, stoneflies, mayflies (Vepsäläinen, 1978; Corkum, 1987; Malmqvist, 2000), and caddisflies (Gullefors & Petersson, 1993; Kovats et al., 1996; Hoffsten, 2004).

Moreover, the life-cycle of Trichoptera requires various functions of the morphology. This morphology changes in evolutionary processes. Hence, information on the size and shape of the body in animal populations, namely in an order of insects, allows to observe how much the

body model of different species can change within a determinate systematic group (Goretti et al., 2005). This approach also makes it possible to identify morphometric variations (Cadrin, 2000) within an order of insects, which may be linked to the species- or genus- or family-specific ecological needs of the species given.

Numerous biometric studies have been conducted on a population or a community of lentic and lotic freshwater invertebrates (e.g. Smock, 1980; Meyer, 1989; Wenzel et al., 1990; Rasmussen, 1993; Robertson, 1995; Dudgeon, 1996; Grubaugh et al., 1997; Fonseca & Esteves, 2000). However, morphometric studies of all the taxa of a faunal group (namely of an order of insects) distributed over large geographical areas are rarely found in literature (Goretti et al., 2005). Aerodynamic theory suggests that several morphological factors could influence flight ability, including total body mass, relative thorax size, wing loading and the AR of the wings (Vogel, 1981). Studies linking caddisflies' morphology, dispersal ability, and distribution are scarce (Gullefors & Petersson, 1993; Kovats et al., 1996; Hoffsten, 2004).

In Trichoptera one general blueprint seems to fit all investigated species as stated in Goretti et al. (2005). This is not reflected in the various dispersal strategies and behaviours recorded for caddisflies. As a consequence, we try to address the following hypothesises on the basis of newly gained flight-morphological data for 86 German Trichoptera species. Additionally, we take known ecological and behavioural information into account and establish links between all information available.

The aim of this thesis is to circumstantiate the following hypothesises

First, flight morphological features characterise dispersal ability and are strongly correlated to each other as the morphology is the basis for any dispersal and every species has a species specific blueprint. This blueprint is expressed in size proportions of morphological features and differs significantly from one genus/family to another because the body blueprint is a mirror to evolutional development lines.

Second, compared to males, caddisfly females are generally considered the dispersing sex, which should reflect in flight morphology patterns typical for strong dispersers and the aerodynamical design of females is more energy-efficient than in males.

Third, when comparing different species, wing morphology reflects the ecological preferences of the species. Ecological generalists will disperse more frequently as the danger of landing in an unsuitable habitat is low.

Last, water bodies differ in their current regime; running waters (lotic) are considered quite stable in time, whereas standing water bodies (lentic) are considered comparably instable. Species inhabiting lentic environment require strategies to compensate the possible loss of a whole population. Consequently these species have a greater urge to disperse than lotic species and this reflects in morphology.

We investigate these hypothesises on three different taxonomic hierarchy levels:

- Chapter 1:

Wing-morphology of selected limnephilid caddisflies (Insecta: Trichoptera: Limnephilidae) in relation to their habitat preferences

The first chapter deals with the central European caddisfly family Limnephilidae. We analysed 26 species in wing morphology and compared the data gained with species-specific ecological information such as habitat preference and stream zone preference. We investigated the material given on mostly on genera-level.

- Chapter 2:

Flight-morphology of four goerid caddisflies (Insecta: Trichoptera: Goeridae) in relation to habitat preferences

This chapter deals with four central European species of the family Goeridae:

Goera pilosa (FABRICIUS, 1775),
Silo nigricornis (PICTET, 1834),
Silo pallipes (FABRICIUS, 1871), and
Silo piceus (BRAUER, 1857)

We compare morphological data on the species level and include weight parameters. The data obtained is related to ecological information available on altitude preference, empergence period duration and stream zone preference.

- Chapter 3:

Flight-morphology of German Trichoptera (Insecta) in relation to their ecological preferences and flight behaviour

This chapter deals with 86 central European caddisfly species belonging to 14 families. We investigate flight-morphological data on the family level and use PCA to link the results with available ecological information such as stream zone preference, emergence period duration and flight behaviour.

1. Wing-morphology of selected limnephilid caddisflies (Insecta: Trichoptera: Limnephilidae) in relation to their habitat preferences

1.1 Introduction

Running water bodies undergo longitudinal changes and the occurrence of species changes in it. The composition and structure of stream biotic communities have been shown to change in response to longitudinal changes in habitat characteristics, such as temperature, current velocity, depth, width, discharge, substratum, turbidity and food availability (Hynes, 1970; Fisher, 1982; Allan, 1996).

One species-rich, widely distributed, amphibiotic insect group, the caddisflies (Insecta: Trichoptera), constitute an important fraction of biomass in most running water ecosystems (Illies, 1958; Waringer, 1986). The Limnephilidae represent one of the largest families within the order of Trichoptera, with more than one third of all European caddisfly species belonging to them (Andersen & Wiberg-Larsen, 1987). It is the dominant group in much of the Northern Hemisphere at higher latitudes and elevations and it is arguably the most ecologically diverse caddisfly family, as larvae occupy the full range of habitats, ranging from lakes, to streams, and marshes (Holzenthal et al., 2007).

The primary purpose of the adult phase of the typical merolimnic insect life cycle is mating and the deposition of eggs in habitats suitable for larval development (Kovats et al., 1996). In the life cycle the terrestrial phase is often quite short and it is the only opportunity to colonise new catchment areas. The entering of new habitats is necessary to ensure the survival of populations through gene transfer. Individuals disperse either actively by flight or passively by wind drift. Most of the time it will be a combination of both movements as the distance between catchments varies in size. The dispersing sex and fecundity state defines the structure of the gene transfer. Dispersing males and immature females enrich the gene pool of an existing unrelated population, but gravid females have the potential to re-colonise new habitats. Important information for these exchange- and colonisation-processes is the range of one dispersing individual which is species-, maybe sex-specific. Unfortunately, information on flight range values in Trichoptera in literature is scarce. Coutant (1982) showed a maximum upstream flight distance of several kilometres for different Hydropsychidae, while Malicky (1987) proved multi-directional flight ranges of several dozens of kilometres and vertical migration in different *Limnephilus*-species. Considerable

variation in dispersal tendencies among species and sexes were also revealed by several population genetic studies (e.g. Waringer, 1989; Bunn & Hughes, 1997; Hughes et al., 1998; Wilcock et al., 2001; Kelly et al., 2002).

All flight movements described are enabled through wings and flight muscles, which represent the basic flight-morphologic equipment. Wainright (1994) stated that morphology and function are often associated. Consequently, morphology may therefore provide a useful indication of dispersal ability (Hoffsten, 2004). Some of these morphological factors are wing length, total wing area, as well as size-independent indices like RWL (RWL), and variously calculated ARs of the wings (Vogel, 1981; Malmqvist, 2000; Lindhe Norberg, 2002). Goretti et al. (2005) proved strong linear relationships between different morphological features within species and the whole data-set. However, empirical evidence linking morphology, dispersal ability, and distribution in aquatic insects is rare, except some studies on wing morphology in water striders, stoneflies, mayflies (Vepsäläinen, 1978; Corkum, 1987; Malmqvist, 2000), and caddisflies (Gullefors & Petersson, 1993; Kovats et al., 1996; Hoffsten 2004).

Broad variation of life cycle styles such as longevity or emphemerallity, habitat generality or specialism, dispersing males or females, and feeding or non-feeding imagines require different dispersal abilities which should be reflected in wing morphology and aerodynamic indices. Some studies prove males as the dispersing sex in *A. fuscipes, L. reducta and S. pallipes* (Sode & Wiberg-Larsen, 1993), while Kovats et al. (1996) found female-biased sex ratios which support the idea of the dispersing females. Already Svensson (1974) stated that the sex-ratio may be associated with species-specific developmental or reproductive behaviour.

Dispersal strategies are adapted to such different habitats like lentic or lotic water bodies. Lentic macroinvertebrates occur in isolated, island-like habitats, separated by inhospitable terrestrial landscape (van de Meutter et al., 2006) and dispersal between lentic habitats may be achieved by active flight or passive dispersal over land (Bilton et al., 2001). On average, if evolutinal time frames are considered, lotic habitats are more stable and predictable over space and time than lentic habitats (Marten, Brändle & Brandl, 2006) and therefore, lentic habitats should be favourably inhabitated by species with higher dispersal capacities which

would ensure population survival of lentic species and should be significantly higher than in lotic species.

This study deals with central European species of the family Limnephilidae, of which 359 species occur in Europe and 100 are registered for Germany (Graf & Schmidt-Kloiber, 2008). We try to address the following hypothesises on the basis of newly gained flight-morphological data for 26 German limnephilid caddisflies by measuring wing length, width, area and body length of 685 specimens. Additionally, we take known ecological information into account and establish links between all information available.

First, we address the hypothesis that wing morphological features characterising dispersal ability are strongly correlated to each other. Second, compared to males, limnephilid females are stronger dispersers, which should be reflected in wing morphology patterns (longer wings, greater wing area, and higher AR). Third, when comparing different species, wing morphology reflects the preferred habitat of the larvae, with species bound to rare and patchily distributed habitats being characterised by a generally weaker dispersal capacity. Finally, wing morphology further reflects the stream zone preferred by the species, with crenal (spring inhabiting) species being poor dispersers compared to species preferring large rivers and lakes.

1.2 Methods

We investigated the wing morphology of adult limnephilid caddisflies from the collections of Thomas Ehlert (2009), Thomas Pitsch and Peter Rolauffs originating from different parts of Germany. Thomas Ehlert collected caddisflies in 1996 and 1997 along the Felderbach, a 4th order brook in the lower mountainous areas of Northrhine-Westphalia (51°21'N 7°10'E). The collection of Thomas Pitsch mainly originates from the Fulda, a 6th order river in Hessen (50°40' N, 9°45' E), and was sampled between 1980 and 1987; some additional specimens were sampled in the Black Forest in Southern Germany in the same period of time. Peter Rolauffs collected caddisflies along a 2nd order mountain brook in the Eifel Mountains (50° 45' N 6° 20' E) in 1998. The collectors used a variety of methods, including light trapping, emergence traps, sweep-netting and hand-picking. All specimens were indentified to the species and sex and preserved in minimum 70 % ethanol until dissection.

Altogether, we investigated 685 specimens representing 341 male and 344 female caddisflies belonging to 26 species and 13 genera of the family Limnephilidae. In 18 cases a total of 15 males and 15 females per species were tested, while in 3 cases the number of specimens was lower but individuals of both sexes were present whereas in 5 cases only specimen of one sex were investigated (Tab. 1.1). The 18 species with 15 individuals per sex were used for further statistical analysis.

All wings of each specimen were disconnected from the thorax at the wing joints with dissection forceps, marked individually, and photographed using a binocular microscope (Olympus SZX9) and camera (moticam 2000 2.0M, produced by Motic China Group 2004). Pictures of the individual wings and the wingless body were taken as colour photos of 800 x 600 pixels resolution. Maximum possible magnification was chosen for each wing. Serial photos were taken of the wings of larger species such as *H. digitatus* if wings could not be pictured entirely at minimum magnification. In these cases the serial pictures were stitched together with the photo stitching software PTGui Pro v8.3 (New House Internet Services B.V., Rotterdam, The Netherlands, 2009) and therefore exceeded the size of 800 to 600 pixels afterwards. Subsequently all colour photos were converted to 8-bit greyscale pictures using Corel Photo-Paint X5 v.15.2.0.661 (Corel Corporation, 2010).

Wing length, width and area as well as body length and span between wing joints were measured to the nearest 0.1 µm using ImagePro Analyzer 6.3 (Media Cybernetics, 2008).

Most Trichoptera couple their fore and hind wings into a single composite aerofoil (Ivanov, 1985; Grodnitsky, 1999; Wootton, 2002). Therefore, wing width is the total of fore and hind wing width, while wing area is the total area of all four wings. Minorly damaged wings were reworked individually during the measurement process. Majorly damaged or missing wings were replaced by the arithmetic mean of the remaining parameter specific values of all measured specimen belonging to the investigated species and sex. In total 30 values were replaced which equal 1% of the total.

The following indices were calculated to characterize wing morphology:

(1) Since body size varies considerably across species an index of RWL was used, which simply equals the ratio of forewing to body length (Malmqvist, 2000).
(2) Aspect ratio I (AR I) is a dimensionless measure wing shape and is calculated by dividing wing length by wing width of the fore and hind wings combined, as the fore and hind wings of caddisflies operate in flight as a single lifting surface (Grodnitsky, 1999).
(3) Aspect ratio II (AR II) is defined as the ratio of the wing span to its mean chord; therefore, it is calculated as wing span squared divided by total wing area and is a dimensionless number (Lindhe Norberg, 2002).
(4) Sexual size dimorphism given as male-to-female wing length ratio according to Gullefors and Petersson (1993) was calculated for all applicable species.

Body length of specimens was allocated to the following groups: small<10.00 mm, 10.00mm<medium<15.00mm, and 15.00mm<big.

All investigated species were assigned values on habitat specialization and stream zonation preference according to the freshwaterecology.info database (Graf & Schmidt-Kloiber, 2008). Here, a habitat specialist is defined to prefer one out of 13 habitat categories, whereas stream zonation preference is coded in a ten point assignment system which is based on the known (or estimated) average distributions, of a taxon within the environmental gradient: if 70% of a species' records are observed in spring brooks and 30% in the upper trout region, 7 out of 10 points will be allocated to the category "hypocrenal" (spring brook) and 3 points to "epirhithral" (upper trout region) (Graf & Schmidt-Kloiber, 2008). These detailed categories were simplified into the broader stream zones crenal,

rhithral, potamal, and littoral; a species was considered as predominantly occurring if 5 or more points were assigned to a category (Tab. 1.1). This information was also assigned to the species which were analysed with the one-way ANOVA.

Biometric parameters such as body length, forewing length, total wing width and total wing area were analyzed by linear regression analysis. The arithmetic means of the parameters were compared using a one-way ANOVA after testing for departures from normality (Kolmogorov-Smirnov and Shapiro-Wilk tests) and homoscedasticity (Levene test). The Scheffé's a posteriori contrast is a commonly used ANOVA post-hoc test for multiple pairwise comparisons of predefined groups with equal group sizes. The Scheffé's contrast was used to identify morphologically homogeneous groups of species within the species-pool tested by the ANOVA. If more than one morphologically homogenous group is identified the formed groups are differing with $p<0.05$ (after Day & Quinn, 1989). The species which formed a homogenous group were displayed in a table and the ecological information of the named species was added.

Sexual dimorphism is widely spread in morphology. Hence, we tested for differences between sexes of one species with an independent t-test. All analyses were conducted with SPSS 18.0 (PASW Statistics 18, 2009) except linear regression analysis for morphologic parameters (SigmaPlot 11.0; Systat Software, 2008) and calculation of coefficients of variation (Statistica 9.0; Statsoft Inc., 2009).

1.3 Results

Species differed strongly in total wing area (72.54-1367.48 mm²), forewing length (7.20-32.21 mm) and total wing width (6.02-29.33 mm), but the dimensionless indices were less variable, i.e. RWL (1.01-1.64), AR I (1.03-1.30), AR II (3.07-5.04), and male-to-female wing ratio (0.82-1.16) (Tab. 1.1 & 1.2). The variation within one species for the parameters measured is given as coefficient of variation (Tab. 1.1); forewing length varies highly in females of *L. lunatus* (CV=14.20) and females of *P. nigricornis* (14.10) whereas males of the spring species *P. picicornis* show high variation in wing width (CV=24.5). Total wing area varies as little as CV=4.14 in *P. cingulatus* males and as much as CV=24.84 in females of *L. lunatus*; variation in body length was highest for *A. nervosa* males (CV=20.01), *H. digitatus* females (20.40), and *D. annulatus* males (27.15; Tab. 1.1). Malicky (2004) gives species- and sex-specific size ranges for forewing length of adult caddisflies; as a whole our measurements are within the ranges, but both sexes of *A. auricollis* are smaller in our measurements and *P. cingulatus*, *P. latipennis*, and *P. nigricornis* are bigger than the ranges given (Tab. 1.1). The males of *S. permistus*, *A. obscurata*, and C*. villosa* exceed the given ranges as well (Tab. 1.1). In general, the morphology is similar within one genus as seen in e.g. in *Drusus* and *Potamophylax*, but in *Limnephilus* the morphological blueprint is very variable (Tab. 1.1).

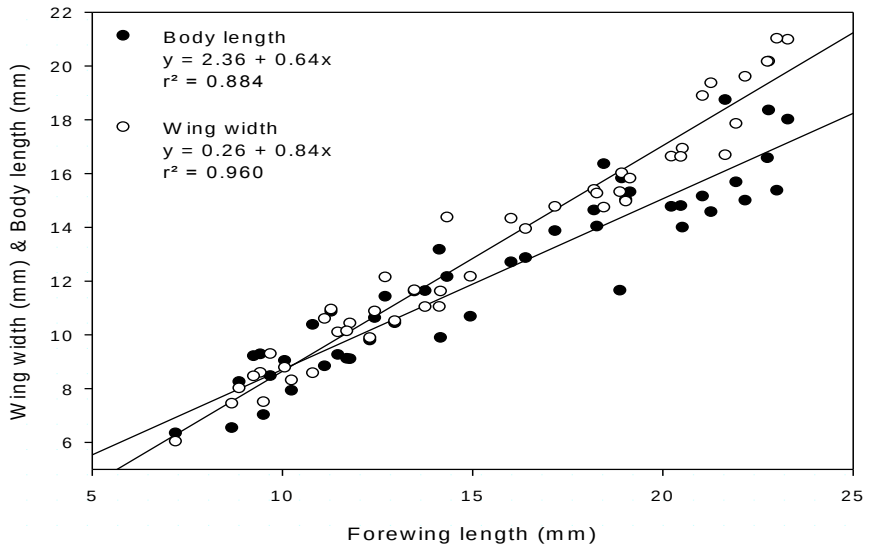

Fig. 1.1: Relationship between forewing length and total wing width and body length. Each circle gives a mean value for the male or the female of a species. Filled circles represent data on forewing length; unfilled circles represent data on total wing width. Linear regression analysis indicated that the slope of the relationship is steeper for forewing length than for total width.

The correlation between the morphological parameters measured was analysed by regression analysis. Despite the overall variability, all wing morphological parameters are strongly related to forewing length (Fig. 1.1 and 1.2). We used the forewing length as an overall measure of size. The wing width increases more strongly with the forewing length (inclination = 0.84; R^2 =0.96) than the total body length (inclination = 0.64; R^2 =0.88; Fig. 1.1). Wing area is strongly related to forewing length (r^2 = 0.88; Fig. 1.2). Hence, there is a strong correlation between each and every morphological parameter tested.

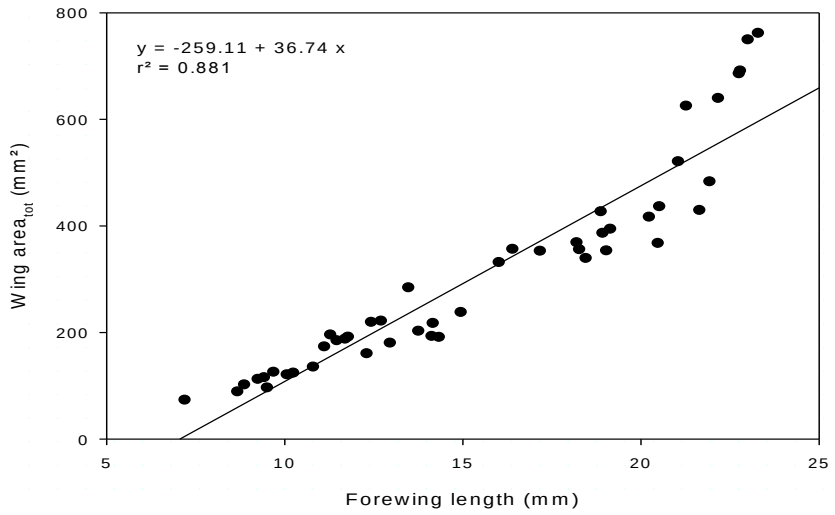

Fig. 1.2: Relationship between forewing length and total wing area. Each circle gives a mean value for the male or the female of a species.

Tab. 1.1: Synopsis of data on morphologic variation of adult limnephilid caddisflies; showing species, number of male (m) and female (f) individuals (n), analysed by ANOVA indicated by a (A), forewing length (mm), FWL forewing length as given in Malicky (2004), cumulative width of fore and hind wing (mm), total area of all wings (mm²), and body length (mm) in arithmetic mean±95% CL and variation coefficient.

				Forewing length		FWL	$Width_{tot}$		$Area_{tot}$		Body length	
Species	Sex	n	A	(mm)	CV	Malicky	(mm)	CV	(mm²)	CV	(mm)	CV
Drusus annulatus	m	15	a	10,80 ± 0,54	2.8	7-13	8,56 ± 0,37	7.9	134,66 ± 16,11	21.6	10,36 ± 1,55	27.2
(STEPHENS, 1837)	f	15	a	9,51 ± 0,29	3.9	7-14	7,48 ± 0,28	6.9	95,67 ± 6,43	12.1	7,01 ± 0,46	11.9
Drusus discolor	m	15	a	9,25 ± 0,19	2.6	9-14	8,44 ± 0,23	5.0	111,70 ± 4,92	8.0	9,20 ± 0,51	10.2
(RAMBUR, 1842)	f	15	a	8,87 ± 0,23	2.8	9-14	8,00 ± 0,20	4.6	101,32 ± 5,10	9.1	8,23 ± 0,26	5.7
Ecclisopteryx dalecarlica												
KOLENATI, 1848	f	15		12,96 ± 0,24	3.1	11-15	10,50 ± 0,17	3.0	179,71 ± 5,07	5.1	10,42 ± 0,18	3.2
Ecclisopterysx guttulata												
(PICTET, 1834)	f	15		12,31 ± 0,50	3.3	11-15	9,87 ± 0,35	6.6	159,86 ± 11,65	13.2	9,78 ± 0,34	6.4
Anabolia nervosa	m	15	a	14,95 ± 0,47	8.4	9-15	12,15 ± 0,34	5.2	237,09 ± 10,12	7.7	10,66 ± 1,18	20.0
(CURTIS, 1834)	f	15	a	14,17 ± 0,26	3.7	9-15	11,60 ± 0,30	4.8	216,72 ± 8,80	7.3	9,87 ± 0,37	6.9
Glyphotaelius pellucidus	m	15		18,20 ± 1,77	3.8	12-17	15,38 ± 1,51	17.8	368,08 ± 47,48	23.3	14,61 ± 1,61	20.0
(RETZIUS, 1783)	f	14		16,40 ± 0,70	8.7	12-17	13,92 ± 0,60	7.5	355,67 ± 25,51	12.4	12,84 ± 0,55	7.5
Limnephilus centralis	m	15		10,25 ± 0,43	2.7	7-10	8,29 ± 0,38	8.4	123,28 ± 14,99	22.0	7,91 ± 0,34	7.8
CURTIS, 1834						7-10						
Limnephilus extricatus	m	15	a	13,48 ± 0,73	8.9	11-14	11,64 ± 0,46	7.2	283,51 ± 31,46	20.0	11,60 ± 0,29	4.6
McLACHLAN, 1865	f	15	a	11,78 ± 0,34	2.4	11-14	10,41 ± 0,34	5.9	190,96 ± 11,40	10.8	9,08 ± 0,36	7.2
Limnephilus flavicornis	m	6		13,76 ± 0,40	5.1	11-14	11,02 ± 0,71	6.1	202,01 ± 20,76	9.8	11,61 ± 0,51	4.2
(FABRICIUS, 1787)						11-17						
Limnephilus fuscicornis	m	15	a	17,17 ± 0,39	2.9	13-16	14,75 ± 0,32	4.0	352,12 ± 12,26	6.3	13,85 ± 0,23	3.0
RAMBUR, 1842	f	15	a	16,02 ± 0,31	6.0	13-16	14,30 ± 0,41	5.3	330,97 ± 9,98	5.4	12,68 ± 0,43	6.1
Limnephilus griseus	m	15		11,47 ± 0,28	1.5	8-13	10,08 ± 0,26	4.7	184,05 ± 6,30	6.2	9,24 ± 0,13	2.6
(LINNAEUS, 1758)						8-13						
Limnephilus lunatus	m	14		14,13 ± 1,04	5.6	9-14	11,03 ± 1,02	4.7	192,36 ± 1,05	8.4	13,15 ± 0,43	5.8
CURTIS, 1834	f	15		14,34 ± 1,08	14.2	9-14	14,35 ± 1,11	18.2	190,54 ± 1,15	24.8	12,14 ± 0,72	10.8
Limnephilus rhombicus	m	15	a	18,46 ± 0,72	4.9	14-19	14,72 ± 0,54	6.7	338,55 ± 21,18	11.3	16,34 ± 0,53	5.9
(LINNAEUS, 1758)	f	15	a	19,04 ± 0,68	3.1	14-19	14,95 ± 0,40	4.9	352,85 ± 21,40	11.0	15,01 ± 0,49	6.0
Limnephilus sparsus	m	15	a	12,43 ± 0,56	4.5	9-12	10,86 ± 0,34	5.8	218,64 ± 14,10	11.6	10,61 ± 0,31	5.4
CURTIS, 1834	f	15	a	11,70 ± 0,48	3.2	9-12	10,12 ± 0,43	7.7	187,07 ± 14,11	13.6	9,09 ± 0,42	8.5
Allogamus auricollis	m	6		9,43 ± 0,67	1.9	11-16	8,57 ± 0,70	7.8	114,89 ± 15,68	13.0	9,26 ± 0,61	6.3
(PICTET, 1834)	f	15		10,07 ± 0,73	7.5	11-16	8,77 ± 0,44	9.1	120,34 ± 13,19	19.8	9,02 ± 0,56	11.3
Halesus digitatus	m	15	a	23,29 ± 0,46	3.5	16-23	20,96 ± 0,41	3.5	761,05 ± 24,98	5.9	17,99 ± 0,69	7.0
(SCHRANK, 1781)	f	15	a	21,27 ± 0,78	3.8	16-23	19,34 ± 0,81	7.6	624,54 ± 56,78	16.4	14,55 ± 1,64	20.4
Halesus radiatus	m	15	a	22,79 ± 1,06	9.6	16-23	20,15 ± 1,41	12.7	690,40 ± 85,62	22.4	18,33 ± 0,65	6.4
(CURTIS, 1834)	f	15	a	23,01 ± 0,38	2.5	16-23	21,00 ± 0,37	3.2	748,84 ± 28,55	6.9	15,35 ± 0,50	5.9
Micropterna lateralis	m	15	a	18,93 ± 0,98	4.5	14-18	16,00 ± 0,74	8.4	385,88 ± 33,77	15.8	15,80 ± 0,78	8.9
(STEPHENS, 1837)	f	15	a	18,27 ± 1,12	3.7	14-18	15,24 ± 0,81	9.7	355,03 ± 38,54	19.6	14,01 ± 0,53	6.8
Parachiona picicornis	m	15	a	7,20 ± 0,96	7.5	7-10	6,02 ± 0,81	24.5	72,53 ± 8,15	20.3	6,32 ± 0,68	19.6
(PICTET, 1834)	f	15	a	8,68 ± 0,36	6.4	6-10	7,43 ± 0,38	9.3	88,16 ± 9,04	18.5	6,52 ± 0,23	6.6
Potamophylax cingulatus	m	15	a	21,05 ± 0,32	2.7	13-20	18,87 ± 0,21	2.0	520,11 ± 11,92	4.1	15,13 ± 0,55	6.6
(STEPHENS, 1837)	f	15	a	20,52 ± 0,46	2.9	13-20	16,91 ± 0,32	3.4	435,64 ± 16,39	6.8	13,98 ± 0,47	6.1
Potamophylax latipennis	m	15	a	21,93 ± 0,73	4.3	13-20	17,83 ± 0,37	3.8	482,32 ± 20,38	7.6	15,66 ± 0,50	5.9
(CURTIS, 1834)	f	15	a	20,23 ± 0,36	4.0	13-20	16,61 ± 0,37	4.1	415,94 ± 14,03	6.1	14,75 ± 0,45	5.6
Potamophylax luctuosus	m	15	a	21,65 ± 0,62	3.9	16-22	16,67 ± 0,53	5.8	428,61 ± 24,99	10.5	18,72 ± 1,03	10.0
(PILLER&MITTERPACHER, 1783)	f	15	a	20,48 ± 0,31	2.7	16-22	16,60 ± 0,30	3.3	366,87 ± 13,15	6.5	14,78 ± 0,54	6.7
Potamophylax nigricornis	m	15	a	19,15 ± 0,78	2.2	13-18	15,80 ± 0,63	7.3	393,39 ± 41,15	18.9	15,29 ± 0,58	7.0
(PICTET, 1834)	f	15	a	18,88 ± 0,67	14.1	13-18	15,29 ± 0,70	8.3	426,25 ± 26,09	11.1	11,63 ± 0,82	12.7
Stenophylax permistus	m	15	a	22,76 ± 0,82	3.5	19-22	20,14 ± 0,60	5.4	685,11 ± 43,38	11.4	16,56 ± 0,81	8.9
McLACHLAN, 1895	f	15	a	22,17 ± 0,66	2.9	21-24	19,58 ± 0,62	5.7	638,87 ± 38,45	10.9	14,98 ± 0,88	10.7
Annitella obscurata	m	15	a	12,71 ± 0,27	2.5	7-12	12,12 ± 0,29	4.4	221,03 ± 10,7	8.7	11,40 ± 0,39	6.3
(McLACHLAN, 1876)	f	15	a	11,12 ± 0,26	3.2	7-14	10,58 ± 0,22	3.8	172,51 ± 6,57	6.9	8,82 ± 0,51	10.5
Chaetopteryx villosa	m	15	a	11,29 ± 0,60	6.5	6-10	10,93 ± 0,57	9.5	194,95 ± 19,93	18.5	10,84 ± 0,38	6.4
(FABRICIUS, 1798)	f	15	a	9,69 ± 0,93	8.0	7-12	9,27 ± 0,89	17.3	125,04 ± 15,56	22.5	8,45 ± 0,59	12.7

Tab. 1.2: Synopsis of data on morphologic variation of adult limnephilid caddisflies; showing species, number of male (m) and female (f) individuals (n), dimensionless indices: RWL, AR I, AR II in arithmetic mean, and male-to-female wing ratio (male forewing length (female forewing length)$^{-1}$); collection information: number of individuals collected by E=Ehlert, P=Pitsch, and R=Rolauffs).

			Relative wing length	Aspect ratio I	Aspect ratio II	male/female ratio	Collector		
Species	Sex	n	(length body^{-1})	(length width^{-1})	(span^2 area$_{tot}^{-1}$)	wing length	E	P	R
D. annulatus	m	15	1,12 ± 0,19	1,26 ± 0,01	4,33 ± 0,29	1.13		15	
	f	15	1,37 ± 0,07	1,27 ± 0,02	4,42 ± 0,12			15	
D. discolor	m	15	1,01 ± 0,04	1,09 ± 0,01	3,63 ± 0,12	1.04		15	
	f	15	1,07 ± 0,02	1,10 ± 0,01	3,68 ± 0,08			15	
E. dalecarlica									
	f	15	1,24 ± 0,02	1,23 ± 0,02	4,37 ± 0,09			15	
E. guttulata									
	f	15	1,26 ± 0,04	1,24 ± 0,02	4,43 ± 0,10			15	
A. nervosa	m	15	1,46 ± 5,52	1,25 ± 0,05	4,25 ± 0,28	1.05	5	10	
	f	15	1,44 ± 0,24	1,22 ± 0,02	4,27 ± 0,17			15	
G. pellucidus	m	15	1,30 ± 0,25	1,18 ± 0,02	4,41 ± 0,68	1.10		15	
	f	14	1,28 ± 0,05	1,18 ± 0,05	3,62 ± 0,21		2	8	4
L. centralis	m	15	1,29 ± 0,02	1,23 ± 0,01	3,99 ± 0,22		2	13	
L. extricatus	m	15	1,16 ± 0,07	1,16 ± 0,05	3,11 ± 0,37	1.14	4	11	
	f	15	1,30 ± 0,03	1,13 ± 0,01	3,39 ± 0,05		1	14	
L. flavicornis	m	6	1,18 ± 0,03	1,25 ± 0,06	4,39 ± 0,30				6
L. fuscicornis	m	15	1,24 ± 0,03	1,16 ± 0,01	3,88 ± 0,11	1.07		15	
	f	15	1,26 ± 0,03	1,12 ± 0,03	3,63 ± 0,10			15	
L. griseus	m	15	1,24 ± 0,02	1,13 ± 0,00	3,37 ± 0,14			15	
L. lunatus	m	14	1,07 ± 0,02	1,28 ± 0,04	4,81 ± 0,23	0.98	3	11	
	f	15	1,18 ± 0,07	1,01 ± 0,08	2,91 ± 0,52			15	
L. rhombicus	m	15	1,13 ± 0,03	1,25 ± 0,03	4,70 ± 0,17	0.96		15	
	f	15	1,26 ± 0,02	1,27 ± 0,02	4,78 ± 0,09			15	
L. sparsus	m	15	1,17 ± 0,04	1,14 ± 0,02	3,34 ± 0,12	1.06		15	
	f	15	1,28 ± 0,03	1,15 ± 0,02	3,42 ± 0,05			15	
A. auricollis	m	6	1,01 ± 0,05	1,10 ± 0,02	3,63 ± 0,08	0.93		6	
	f	15	1,12 ± 0,07	1,14 ± 0,04	3,95 ± 0,26			15	
H. digitatus	m	15	1,29 ± 0,05	1,11 ± 0,02	3,23 ± 0,08	1.09		15	
	f	15	1,49 ± 0,10	1,10 ± 0,02	3,30 ± 0,10			15	
H. radiatus	m	15	1,24 ± 0,06	1,14 ± 0,06	3,58 ± 0,42	0.99		15	
	f	15	1,50 ± 0,03	1,09 ± 0,01	3,20 ± 0,07			15	
M. lateralis	m	15	1,19 ± 0,04	1,18 ± 0,02	4,22 ± 0,17	1.03	8	7	
	f	15	1,30 ± 0,04	1,19 ± 0,02	4,27 ± 0,12		8	7	
P. picicornis	m	15	1,21 ± 0,25	1,19 ± 0,05	3,58 ± 0,66	0.82		15	
	f	15	1,33 ± 0,06	1,17 ± 0,04	3,99 ± 0,23			15	
P. cingulatus	m	15	1,39 ± 0,06	1,11 ± 0,01	3,72 ± 0,09	1.02		15	
	f	15	1,47 ± 0,04	1,21 ± 0,01	4,39 ± 0,11			15	
P. latipennis	m	15	1,40 ± 0,05	1,23 ± 0,02	4,56 ± 0,17	1.08		15	
	f	15	1,37 ± 0,04	1,21 ± 0,02	4,47 ± 0,10			15	
P. luctuosus	m	15	1,16 ± 0,06	1,29 ± 0,02	5,04 ± 0,13	1.05	15		
	f	15	1,39 ± 0,06	1,23 ± 0,01	4,23 ± 0,07		12	3	
P. nigricornis	m	15	1,25 ± 0,06	1,21 ± 0,01	4,31 ± 0,12	1.01	1	14	
	f	15	1,64 ± 0,10	1,20 ± 0,09	4,31 ± 0,94			15	
S. permistus	m	15	1,38 ± 0,05	1,13 ± 0,02	3,44 ± 0,10	1.02	2	13	
	f	15	1,49 ± 0,07	1,13 ± 0,01	3,50 ± 0,07			15	
A. obscurata	m	15	1,11 ± 0,03	1,04 ± 0,01	3,43 ± 0,07	1.14		15	
	f	15	1,27 ± 0,08	1,05 ± 0,01	3,35 ± 0,09			15	
C. villosa	m	15	1,04 ± 0,03	1,03 ± 0,03	3,07 ± 0,13	1.16		15	
	f	15	1,14 ± 0,07	1,04 ± 0,04	3,65 ± 0,56			15	

Sexual dimorphism is species specific. In terms of forewing length 12 of 18 species analysis showed significant differences between sexes (Tab. 1.3, Fig. 1.3a-c); in case of 11 cases forewings of males are longer, in case of *P. picicornis* forewings of females are longer and in case of *L. rhombicus*, *H. radiatus*, *M. lateralis*, *P. cingulatus*, *P. nigricornis* and *S. permistus* there was no difference. In 9 cases wings of males are wider; in case of *P. picicornis* wings of females are wider, whereas for the remaining 8 species there was no difference (Tab. 1.3, Fig. 1.3a-c). Three of 18 species (*D. annulatus*, *A. nervosa*, *P. picicornis*) showed no significant difference in body length and for all other species males were bigger than females (Tab. 1.3, Fig. 1.3a-c). Wing area is generally larger for males (11 of 18 species); only for *P. picicornis* females have larger wings and for five species there was no difference (*D. discolor*, *L. rhombicus*, *H. radiatus*, *M. lateralis*, and *S. permistus*). RWL differs significantly in 13 of 18 cases and in all cases females exceed males. The aerodynamic indices AR I and II are relatively similar between sexes; nevertheless, in *D. annulatus*, *D. discolor*, and *P. luctuosus* females exceed males (Tab. 1.3) whereas in *L. fuscicornis* and *P. cingulatus* it is vice-versa. As a whole this states that the limnephilid females are not bigger than males. There only exception to this pattern is *P. picicornis* where females do exceed males in all measured parameters.

According to morphological parameters as well as aerodynamic indices except AR I *P. picicornis* females exceed males in all parameters tested, but in *A. obscurata* and *D. discolor* males exceed females (Tab. 1.3, Fig. 1.3a-c). The 18 species investigated belong to eleven genera; given that the allocation of species to a genus represent a closer relation than to other species of the same family but other genera higher similarity in morphological parameters should be provable. In Fig. 1.3d the size-independent values of RWL was correlated to wing area and all values were assigned to the corresponding genus. No distinction between sexes or species was made. A belt-like allocation of values belonging to one genus is clearly visible. The genera *Parachiona* and *Drusus* are well separated in spite of RWL and wing area from the genera *Potamophylax* and *Halesus* for example. These results proved significant ($p<0.05$) in the Scheffe's a posterior contrast.

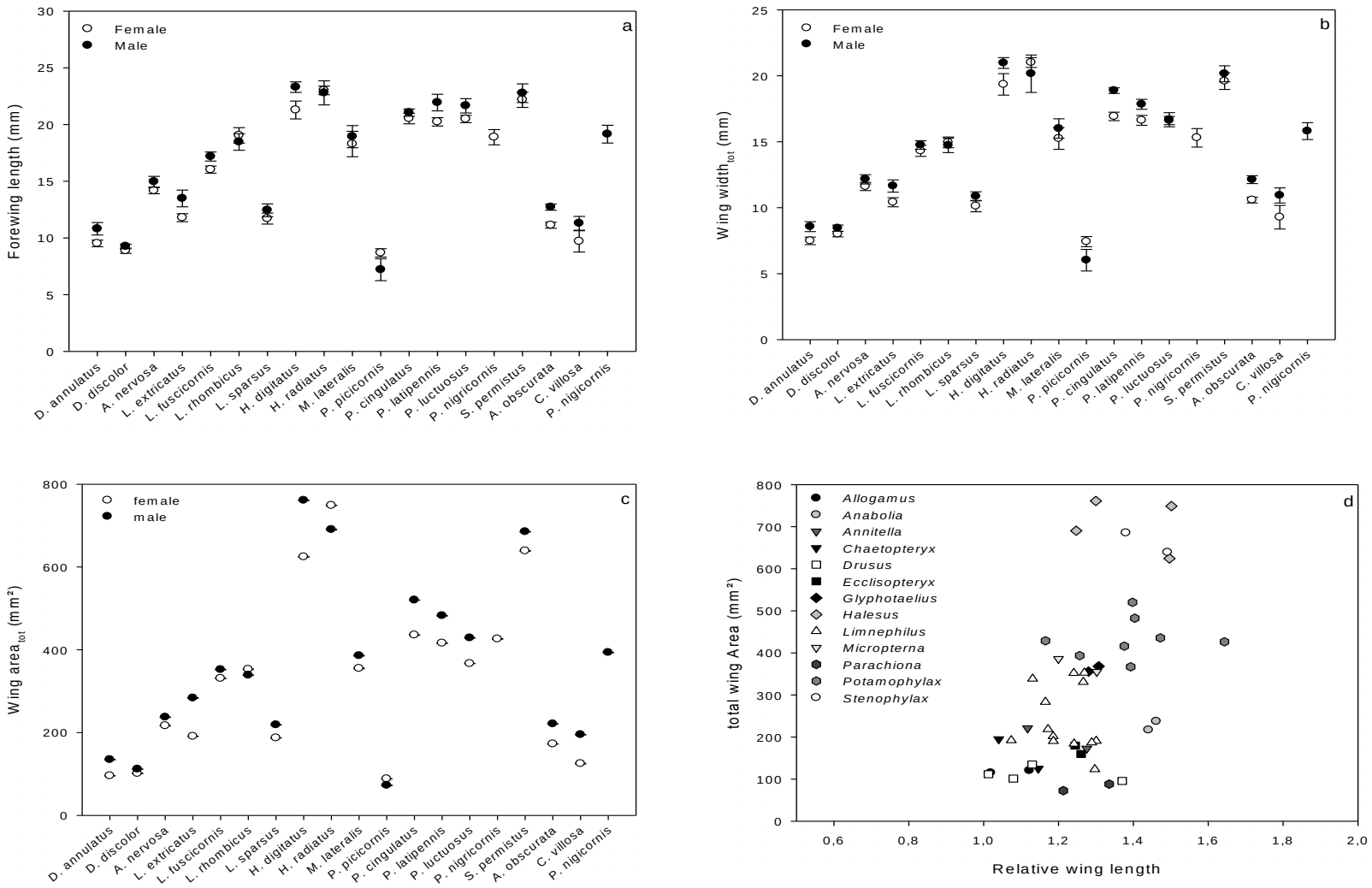

Fig. 1.3 a-d: Wing morphology comparing sexes of individual species; showing arithmetic means with 95% CL error bars of a-forewing length (mm), b-total wing width (mm), and c-total wing area (mm); d showing the relationship between RWL and total wing area (mm); d showing the relationship between RWL and total wing area (mm²) indicating the genus of all tested species.

Tab. 1.3: Differences between sexes of means of morphologic measurements and indices tested with t-test; ns=not significant, *= p<0.05, **= p<0.01, *** p<0.001).

Species	Forewing length		$Width_{tot}$		$Area_{tot}$		Body length		Relative wing Length		Aspect ratio I		Aspect ratio II	
D. annulatus	m > f	***		ns	m > f	**		ns		ns	f > m	***	f > m	***
D. discolor	m > f	***	m > f	**		ns	m > f	***	f > m	***	f > m	***	f > m	***
A. nervosa	m > f	**	m > f	*	m > f	**		ns		ns		ns		ns
L. extricatus	m > f	***	m > f	***	m > f	***	m > f	***	f > m	**		ns		ns
L. fuscicornis	m > f	***		ns	m > f	**	m > f	***		ns	m > f	*	m > f	**
L. rhombicus		ns		ns		ns	m > f	***	f > m	***		ns		ns
L. sparsus	m > f	*	m > f	**	m > f	**	m > f	***	f > m	***		ns		ns
H. digitatus	m > f	***	m > f	**	m > f	***	m > f	***	f > m	**		ns		ns
H. radiatus		ns		ns		ns	m > f	***	f > m	***		ns		ns
M. lateralis		ns		ns		ns	m > f	***	f > m	**		ns		ns
P. picicornis	f > m	**	f > m	**	f > m	*		ns		ns		ns		ns
P. cingulatus		ns	m > f	***	m > f	***	m > f	**	f > m	*	f > m	***	f > m	***
P. latipennis	m > f	***	m > f	***	m > f	***	m > f	**		ns		ns		ns
P. luctuosus	m > f	**		ns	m > f	***	m > f	***	f > m	***	m > f	***	m > f	***
P. nigricornis		ns		ns		ns	m > f	***	f > m	***		ns		ns
S. permistus		ns		ns		ns	m > f	**	f > m	*		ns		ns
A. obscurata	m > f	***	m > f	***	m > f	***	m > f	***	f > m	*		ns		ns
C. villosa	m > f	**	m > f	**	m > f	***	m > f	***	f > m	*		ns		ns

After performing a one-way ANOVA (forewing length F=313.38, p<0.001; total wing width F=249.75, p<0.001) on all parameters measured, we analysed every parameter on its own with the Scheffé post-hoc test to find morphologically homogenous groups. Scheffé's post hoc test produced different groups for all parameters tested. We selected forewing length and wing width (Tab. 1.5) because more than one group was found within the data given and because forewing length is commonly used for the size identification of species. The Scheffé-groups are displayed in Tab. 1.5; in this Tab. 1.5 we added the species-specific ecological information, which was taken and condensed from freshwaterecology.info (Graf & Schmidt-Kloiber, 2008; Tab. 1.4)

Tab. 1.4: Synopsis of information retrieved and concentrated from freshwaterecology.info (Graf & Schmidt-Kloiber, 2008); showing: parameter = ecological parameter, Code = assigned code for calculated stream region, Abbreviation = abbreviation used in the database, and Explanation = as given in the database.

Parameter	Code	Abbreviation	Explanation
habitat specialist		CPOM	coarse particulate organic matter
		lithal	xxxx
		organic habitats	xxxx
		phytal	xxxx
		psammalpelal	sand (grain size 0.063-2 mm) & mud (grain size < 0.063 mm)
stream zone preferences	KRE	eucrenal	spring region
		hypocrenal	spring-brook
	RHI	epirhithral	upper-trout region
		metarhithral	lower-trout region
		hyporhithral	grayling region
	POT	epipotamal	barbel region
		metapotamal	bream region
		hypopotamal	brackish water region
	LIT	profundal	bottom of stratified lakes
		littoral	lake and stream shorelines, lentic sites, ponds etc.
	IND	indifferent	no destinct preferation

With our third hypothesis we stated that species bound to rare and patchily distributed habitats are characterised by a weaker dispersal capacity. Hence, we have taken habitat preferences into account as well. We found similar morphometry in forewing length and wing width in crenal species, of which all are specialists for a mineralic habitat (psammopelal, lithal; Tab. 1.5). In morphometry *C. villosa* is similar to the crenal group, but there is no habitat specialism known for it (Tab. 1.5). The second group of morphologically similar species (forewing length) share the specialisation in organic habitats (phythal, CPOM; Tab. 1.5), but they do not share a common stream zone preference or body size. The third group identified belongs to the rhithral stream zone, except *L. rhombicus* and *P. nigricornis*, but all do not share either body size or habitat preference (Tab. 1.5).

Tab. 1.5: Synopsis of Scheffe's contrast (p<0.05) between significantly different species groups with associated ecology traits based on forewing length and total wing width; showing species, sex, stream zonation preference (KRE=crenal, RHI=rhithral, LIT=littoral, POT=potamal, IND=indifferent), body size (small<10.00 mm, 10.00 < medium < 15.00 mm, big>15.00 mm), and habitat binding.

	Forewing length					Wing width tot			
Species	Sex	Zone	Size	Habitat	Species	Sex	Zone	Size	Habitat
P. picicornis	m	KRE	Small	Psammopelal	*P. picicornis*	m	KRE	Small	Psammopelal
P. picicornis	f	KRE	Small	Psammopelal	*P. picicornis*	f	KRE	Small	Psammopelal
D. discolor	m	KRE	Small	Lithal	*D. discolor*	f	KRE	Small	Lithal
D. annulatus	m	KRE	Small	Lithal	*D. discolor*	m	KRE	Small	Lithal
D. discolor	f	KRE	Small	Lithal	*D. annulatus*	m	KRE	Small	Lithal
C. villosa	f	RHI	Medium		*D. annulatus*	f	KRE	Medium	Lithal
L. extricatus	m	IND	Small	Phythal	*A, obscurata*	m	RHI	Small	
A. nervosa	f	POT	Medium	CPOM	*A. nervosa*	m	POT	Small	CPOM
A. nervosa	m	POT	Small	CPOM	*L. fuscicornis*	f	LIT	Medium	Phythal
L. fuscicornis	f	LIT	Medium	Phythal					
					P. cingulatus	f	RHI	Big	
L. rhombicus	f	LIT	Big	Phythal	*P. latipennis*	m	RHI	Medium	
P. nigricornis	m	KRE	Medium		*P. cingulatus*	m	RHI	Big	
P. latipennis	f	RHI	Medium		*H. digitatus*	f	RHI	Big	org habitats
P. luctuosus	f	RHI	Big						
P. cingulatus	f	RHI	Big						
P. cingulatus	m	RHI	Big						
H. digitatus	f	RHI	Big	org habitats					
P. luctuosus	m	RHI	Medium						
P. latipennis	m	RHI	Medium						

Our last hypothesis was that spring inhabiting species are poor dispersers compared to species inhabiting large rivers and lakes. The Scheffé-test found morphologically similar species inhabiting the crenal and a separated group inhabiting the rhithral in both parameters analysed. The crenal group consists of both sexes of *P. picicornis*, *D. discolor* and *D. annulatus* in wing width. In wing length the crenal group consists mainly of the same species, but *D. annulatus* females are replaced by *C. villosa* females. *P. cingulatus* (both sexes) and the females of *P. latipennis* and *H. digitatus* build a group of rhithral species in wing width. In forewing length the rhithral group is bigger; it consists of the already named species and *P. latipennis* (females), *P. luctuosus* (both sexes), *P. nigricornis* (males), and *L. rhombicus* (females).

We found no groups in the aerodynamical indices AR I and II and in RWL. Hence, we can support our hypothesis only on the analysis of forewing length and wing width, which are only measures of size, but not of function.

1.4 Discussion

Merolimnic insects in the adult stage must find suitable larval habitats for the survival and/or further dispersal of their population. The dispersal ability manifests in different scales: morphology defines the flight ability itself and behaviour defines the percentage of dispersing individuals (male or female). We measured flight morphological parameters and compared size-independent aerodynamic indices to test if differences in structural design can be determined and linked to species-specific ecological requirements.

According to basic aerodynamic principles, morphology can have strong effects on flight ability (Hoffsten, 2004). Due to the fact that preserved material was used for this study the main focus was on morphological parameters and indices, such as forewing length, wing area, RWL, male-to-female wing ratio and ARs. Kovats (1990) proved a very strong linear relationship between forewing length and forewing area ($R^2 \geq 0.97$) for five North American Hydropsychidae species and Goretti et al. (2005) found a very strong linear relationship between forewing length and body length (R^2=0.96; ln transformed) for 961 individuals belonging to 327 Italian caddisfly taxa. We tested individuals of 26 different species belonging to 13 genera of Limnephilidae and compared the arithmetic means of measured flight parameters. We found strong relationships between forewing length and body length (r^2=0.884) and forewing length and wing area (r^2=0.881), but the relationship between forewing length and wing width (r^2=0.960) was even stronger. These relationships justify the common use of forewing length for identification of the size of a species in the order Trichoptera (Malicky, 2004; Goretti et al,. 2005). Malicky (2004) gives ranges for nearly every European species and sex. In most cases our data is within the ranges described by Malicky (2004); in at least one sex of *G. pellucidus*, *L. fuscicornis*, *M. lateralis*, *P. cingulatus*, *P. latipennis*, *P. nigricornis*, and *C. villosa* the measured values are higher, whereas in *A. auricollis* the values measured are lower than the given range. The values given by Goretti et al. (2005) are higher in *L. flavicornis* and *A. auricollis* and lower in *H. digitatus* and *H. radiatus* compared to our values. This is probably due to the small sampling size of this study (three or less specimen per species and sex).When the wing area is considered on the size-independent scale of RWL species belonging to the same genus cluster together (Fig. 1.3d). This supports the hypothesis that dispersal ability evolved differently in different genera of Limnephilidae.

Our second hypothesis stated that females are the dispersing sex in limnephilid caddisflies, which is expressed in longer forewings, greater wing area, and higher ARs. Only in *P. picicornis* females exceed males in forewing length, wing width and wing area, but there is no difference in all other tested parameters, including the aerodynamic indices. No sexual dimorphism in forewing length, wing width, and wing area is present in *L. rhombicus*, *H. radiatus*, *M. lateralis*, *P. nigricornis*, and *S. permistus*. In most (11 of 18; *D. annulatus*, *D. discolor*, *A. nervosa*, *L. extricatus*, *L. fuscicornis*, *L. sparsus*, *H. digitatus*, *P. latipennis*, *P. luctuosus*, *A. obscurata* and *C. villosa*) species, males have longer forewings than females and in all but one (*D. discolor*) of these species the wing area differs between sexes as well (Tab. 1.3).

Male bodies are bigger in all but two cases, *D. annulatus* and *A. nervosa*, where no difference is found. However, females will change their body length during their adult life cycle, depending on their fecundity state (immature, gravid and spent). Since we have no record of the fecundity state of the investigated material, this feature is inadequate as a reliable indicator for sexual dimorphism. Additionally, the fixation of the material might change the body length, as fat and muscle are soluble in ethanol. Hence, it is more reliable to use wing parameters for the analysis of sexual dimorphism in fixed material. The relative wing length (RWL) is one such fixation-independent factor. Interestingly, females have a higher RWL in all species apart from *D. annulatus*, *A. nervosa*, *L. fuscicornis*, *P. picicornis* and *P. latipennis*. ARs are interpreted as a measure of aerodynamic efficiency and higher AR values reduce the lift coefficient at a constant angle of attack by making the wings longer and thinner (Lindhe Norberg, 2002). Therefore, we find a clear advantage for dispersal of females in *D. annulatus*, *D. discolor* and *P. cingulatus*. Strategies of dispersal in various fecundity states would be the acquisition of new habitats with given genetic equipment (fertilised eggs) or the acquisition of a new habitat and genetic material (unfertilised eggs).

Based on AR I and II, *L. fuscicornis* and *P. luctuosus* males have an advantage in dispersal, but the remaining species do not show differences in aerodynamic indices. Dispersal of males would be more energy efficient as eggs, either fertilised or unfertilised are ballast on dispersing individuals.

On the basis of our data we conclude that females disperse in *D. annulatus*, *D. discolor*, *P. picicornis*, and *P. cingulatus*, but no clear indication for a dispersing sex is found in

L. rhombicus, *H. radiatus*, *M. lateralis*, *P. nigricornis* and *S. permistus*. In the remaining species, males appear as dispersers. Hence, the hypothesis is not entirely supported and the picture is more complex than initially anticipated. This is also stated by contradictory observations documented in the literature. Although little information is available on flight behaviour of male limnephilid caddisflies, females in different stages of reproductive development (immature, gravid and spent) in a Swedish stream exhibit non-random inland distribution (Svensson, 1974).

Stream insect larvae often strongly prefer a habitat, e.g. stones (lithal), sand (psammal) or CPOM. We tested the hypothesis that habitat specialists are generally weaker dispersers, as the probability of landing at a suitable habitat will be low. Generalists may disperse more frequently, as more habitats are suitable for their larval development. The Scheffe's test grouped ($p<0.05$) crenal habitat specialists (*P. picicornis*, *D. discolor*, *D. annulatus* and *C. villosa*) in forewing length as well as in wing width. Accordingly, a group of generalistic rhithral species (*L. rhombicus*, *P. nigricornis*, *P. latipennis*, *P. luctuosus*, *P. cingulatus* and *H. digitatus*) was formed in both parameters; these species where of larger body size, wing length, width and area. We found no group summing species of a lentic habitat. Hence, our results support the hypothesis that generalists are stronger dispersers compared to specialists.

Finally, we stated that the wing morphology of inhabiting species is influenced by the stream zone, with crenal species being poor dispersers compared to species preferring large rivers and lakes. Suitable larval habitats can be found in the vicinity, as well as in greater distance to the dispersing population, depending on the ecological requirements of the dispersing species and the habitat's temporally stability. Although some lakes are very old (e.g. Lake Baikal: 25–30 million years, Lake Ohrid: 2–3 million years; Martens, 1997), on an evolutionary timescale lotic habitats are on average more predictable over space and time than lentic habitats (Marten et al., 2006). Clear evidence for the long persistence of rivers and streams is the formation of valleys during thousands or millions of years (e.g. River Elbe and Danube more than 20 million years; Hantke, 1993). Furthermore, during climatic fluctuations, species living in lotic habitats are able to shift their range within drainages, whereas lentic species without terrestrial phase are trapped (Marten et al., 2006). These differences in spatial and temporal persistence between lentic and lotic habitats should

result in consistent differences in dispersal strategies between species living in lentic and lotic habitats: lentic species should show a higher dispersal propensity than lotic species (Ribera & Vogler, 2000). Therefore, one would expect morphology adapted to longer distance dispersal in species bound to lentic habitats. However, for lentic limnephilid caddisflies we found no advantage for dispersal in either morphologic parameters or aerodynamic indices. In contrast to Odonata, which are considered strong active fliers, long-distance dispersal of Trichoptera might be more dependent on passive mechanisms, e.g. wind drift, which is not necessarily reflected in wing morphology. However, parameters such as forewing length and AR might reflect a species' capability of crossing short to medium distances.

Rivers are characterized by longitudinal changes from the crenal (springs) to the potamal (large rivers) with springs offering fairly constant conditions, while small to medium-sized streams (rhithral) are more strongly fluctuating and large rivers are characterized by intermediate levels of disturbance. Hence, one hypothesis is that species inhabiting similar river zones should have similar dispersal abilities; crenal species are considered poor fliers, rhithral species are strong fliers and potamal species have intermediate dispersal capacities. In terms of forewing length and wing width we found species groups of similar morphology inhabiting the crenal and the rhithral, but no group of similar morphology inhabiting the potamal was identified. Crenal species (*P. picicornis*, *D. discolor*, *D. annulatus* and *C. villosa)* are generally small, whereas rhithral species (*L. rhombicus*, *P. nigricornis*, *P. latipennis*, *P. luctuosus*, *P. cingulatus*, and *H. digitatus*) are larger.

Apart from these results, there are other variables than wing morphology determining dispersal capacity, e.g. weather conditions (Briers et al., 2003), precipitation (Waringer, 1991) and wind direction (Usseglio-Polatera, 1987). Furthermore, Limnephilids are considered highly vagil with extended vertical migration (Malicky, 1987) and prolonged flight periods (Waringer, 1991).

In conclusion, our results show that forewing length is a suitable indicator for the species size, that the sex is one determinant of dispersal. However, we found the dispersing sex to be different between species. Additionally, we showed that wing morphology reflects the stream zone and, to some degree, the preferred habitat but could not indicate a preference for lakes or rivers.

Hence, an overall appraisal of dispersal capability needs to consider morphological aspects but also additional variables (e.g. behaviour).

2. Flight-morphology of four goerid caddisflies (Insecta: Trichoptera: Goeridae) in relation to their habitat preferences

2.1 Introduction

Goerid caddisflies are best known for their larvae. They construct heavy, bulky cases and live in running waters, ranging from small cold springs to rivers (König & Waringer, 2008). The family Goeridae encompasses 10 genera with approximately 100 species worldwide (Wiggins, 1998). This study deals with central European species of the family Goeridae, of which 17 species occur in Europe and the following six are registered for Germany: *Goera pilosa* (FABRICIUS, 1775), *Lithax niger* (HAGEN, 1859), *Lithax obscurus* (HAGEN, 1859), *Silo nigricornis* (PICTET, 1834), *Silo pallipes* (FABRICIUS, 1871), and *Silo piceus* (BRAUER, 1857) (Graf & Schmidt-Kloiber, 2008). We investigated four species: *G. pilosa* and the three *Silo*-species. *G. pilosa* inhabits lentic environments like hyporhithral, epipotomal, and littoral. The *Silo*-species mainly inhabit overlapping lotic environments along the longitudinal stream zones. *S. nigricornis* is present most upstream in the hypocrenal and epirhithral, followed by *S. pallipes* in epi- and metarhithral, and most downstream *S. piceus* in meta- and hyporhithral (Graf & Schmidt-Kloiber, 2008).

All goerid larvae are specialists for mineralic habitats but differ in their preferred altitude and current regime: the *Silo*-species are rheophile and prefer the submontane to colline belt whereas the limnophil *G. pilosa* is also found in the lowlands (Graf & Schmidt-Kloiber, 2008). Ehlert (2009) found all *Silo*-species to occur at the same sampling site with wide temperature amplitude and hence, all *Silo*-species are considered to be eurytherm. Graf & Schmidt-Kloiber (2008) identified *G. pilosa* to be eurytherm as well. All goerid species are predominantly grazers/scrapers feeding on epilithic algae (König & Waringer, 2008), but seldom gather and collect sedimented fine particulate organic matter (Graf & Schmidt-Kloiber, 2008). Epilithic algae reach their highest densities where hydraulic stress and water current is highest and therefore, *Silo*-species are required to reach these regions and resists the hydraulic environment (König & Waringer, 2008). *S. nigricornis* was significantly ($p<0.05$) under-represented in drift samples (Waringer, 1992) and drift resistance experiments proved energy efficient drift resistance due to the family specific

case building behaviour (König & Waringer; 2008). In addition, a function as lateral barriers against predators was discussed as well (e.g. Johansson, 1986; Otto & Johansson, 1995). Apart from the well known larval life cycle, information on the terrestrial phase of the goerid life cycle is rare in literature. Svensson (1972) stated that adult life is short, approximately 1-2 weeks. During this period of time individuals do either disperse or stay put.

Concerning adult dispersal of goerid species contradictory observations are documented. *S. pallipes* is found mostly above a brook and in the bankside vegetation, but only rarely as far as 20-40 m from the brook (Sode & Wiberg-Larsen, 1993). The authors also found constant significant emergence deficiency in female *S. nigricornis* (11.5%) and *S. pallipes* (37.9%) during the whole emergence period. Malicky (1987) reported frequently capturing *S. nigricornis* at a distance of 100 m from the nearest larval habitat. Ehlert (2009) found distinct time patterns for flight activity in *S. nigricornis*: males fly during daytime at noon and during the afternoon, whereas the females fly during twilight. In *S. piceus* flight activity of males and females occurs at twilight (Ehlert, 2009). Another aspect is the timespan available for dispersal. Low dispersal may also be a consequence of the short lifespan of some adult Trichoptera (Sode & Wiberg-Larsen, 1993). *S. pallipes* mates soon (hours or days) after emergence (Svensson, 1972; Elliot, 1982). Oviposition occurred in the early evening and night, and usually took 4-6 h to complete (Elliott, 1982). Ross (1944) stated that some teneral (immature adult) caddisflies move inland, where they may rest until they become sexually mature. Strategies for dispersal in various fecundity states would be the acquisition of new habitats with given genetic equipment (fertilized eggs) or the acquisition of a new habitat and genetic material (unfertilised eggs). Dispersal of males would be more energy efficient as eggs, either fertilised or unfertilised, are ballast on dispersing individuals.

Consequently, we want to clarify the dispersal capacity of the species investigated. We use two approaches: one approach is a pure biometric study of the wings and associated weight parameters and the other is an experimental approach quantifying flight distance and flight performance on a species-sex level.

We address these hypotheses by measuring flight-morphology and mass parameters of 90 specimens comprising four goerid species and by matching the resulting adult morphometry and aerodynamic indices to the species ecological preferences. First, we address the hypothesis that wing morphological features and weight parameters characterising dispersal

ability are strongly correlated to each other as the morphology is the basis for any dispersal and every species has a species specific blueprint. Second, compared to males, caddisfly females are generally considered the dispersing sex, which should reflect in wing morphology patterns typical for strong dispersers and the corresponding weight features. Third, dispersal consists of distance travelled actively (flight) and distance travelled passively (wind drift) by the individual. Species bound to more instable habitats like the rhithral as compared to the crenal are expected to have a bigger portion of active distance travelling due to the urge to reach new habitats. Finally, when comparing the species, the preferred altitude, stream zone, and emergence period of the larvae influence the wing-morphology. Species bound to higher elevated altitudinal belts, inhabiting the crenal stream zone and/or showing shorter emergence periods are considered weaker dispersers; this should be reflected in the morphology.

2.2 Methods

2.2.1 Sampling area and material provenance

We investigated the wing morphology of the following adult goerid caddisflies: *G. pilosa*, *S. nigricornis*, *S. pallipes* and *S. piceus*. The individuals of *G. pilosa* were taken from the collection of Thomas Pitsch which originates from the Fulda, a 6th order river in Hessen (50°40’ N, 9°45’ E). The specimens investigated were sampled in 1981 by a variety of methods, including light trapping, emergence traps, sweep-netting and hand-picking, identified to the species and sex, and preserved in 70 % ethanol. The individuals of the genus *Silo* were collected as fifth instar larvae and pupae on the 10th of April 2010 by hand from the stream bottom using forceps. The sampling water body was the Felderbach (51°21’N 7°10’E), a 4th order brook in the lower mountainous areas of Northrhine-Westphalia.

2.2.2 Breeding of Silo spp. in the climate chamber

Larvae and pupae of *Silo* spp. were transported to Essen University in a cooler half-filled with strongly aerated brook water. In the laboratory, at maximum 15 individuals were transferred to one plastic aquarium half-filled with cooled brook water. The aquaria were equipped with a fine layer of gravel on bottom from the brook, then placed in a climate chamber at 10 °C at

the beginning and the water was strongly aerated (Fig. 2.1) (König & Waringer, 2008). Larvae were fed with moss and biofilm from leaves originating from the Felderbach. The light regime in the climate chamber resembled 14 hour daylight and the temperature inside was raised to 14°C in 1 degree steps over 4 weeks to accelerate development of larvae and pupae. Aquariums were checked daily for emergence of individuals. Emerged adults were collected with tubes from aquariums and tubes were marked and stored individually at 8°C in a fridge without internal lighting. Newly emerged individuals were allowed to dry for several hours before. Within 24 hours after emergence individuals were tested for flight performance in the flight chamber.

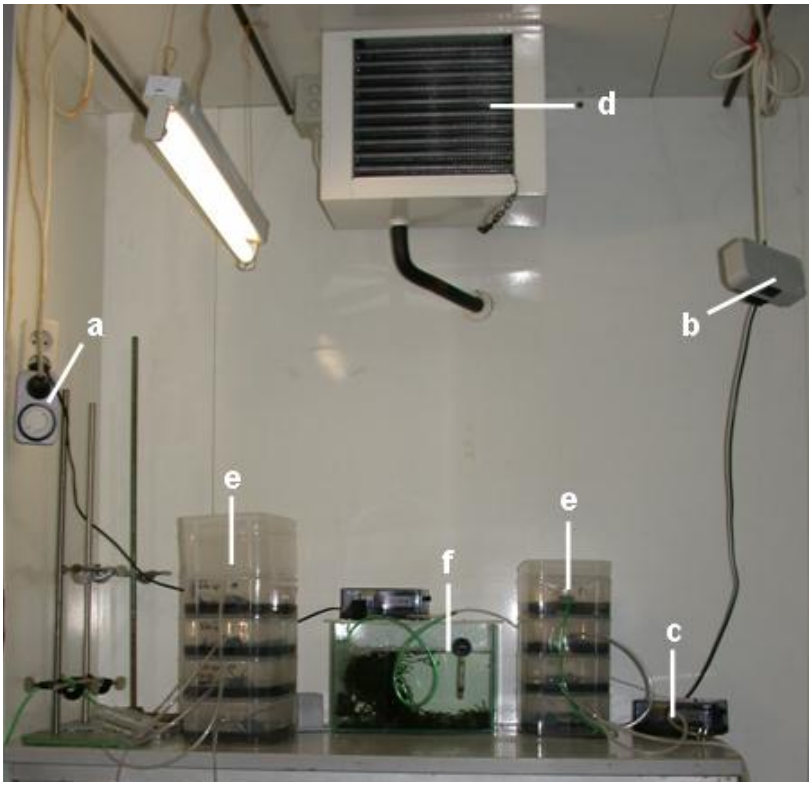

Fig. 2.1: Climate chamber equipped with species-specific breeding aquaria for Trichoptera; a = timer for lighting, b = power supply for diaphragm pump, c = diaphragm pump, d = cooling unit, e = aquaria towers, and f = food aquarium.

2.2.3 Flight performance experiment under laboratory conditions

The dispersal of individuals serves the purpose of the acquisition of new habitats and the compensation of drift loss. The re-colonisation of new habitats is necessary to ensure the survival of a population. In literature little is known about the adult phase of goerid

caddisflies (Mackereth, 1960; Elliot, 1982) and the flight distance travelled by individuals of various species belonging to the Goeridae (Sode & Wiberg-Larsen, 1993). Therefore, we developed a flight performance experiment to quantify the individual yet species-specific flight range. The experiment was operated under laboratory conditions. The whole experimental section (rotating and central beam) for flight performance is housed in a cylindrical Plexiglas containment (Fig 2.2). The containment bears multiple borings in regular intervals which are equipped with a velocity adjustable LED running light (Fig. 2.3).

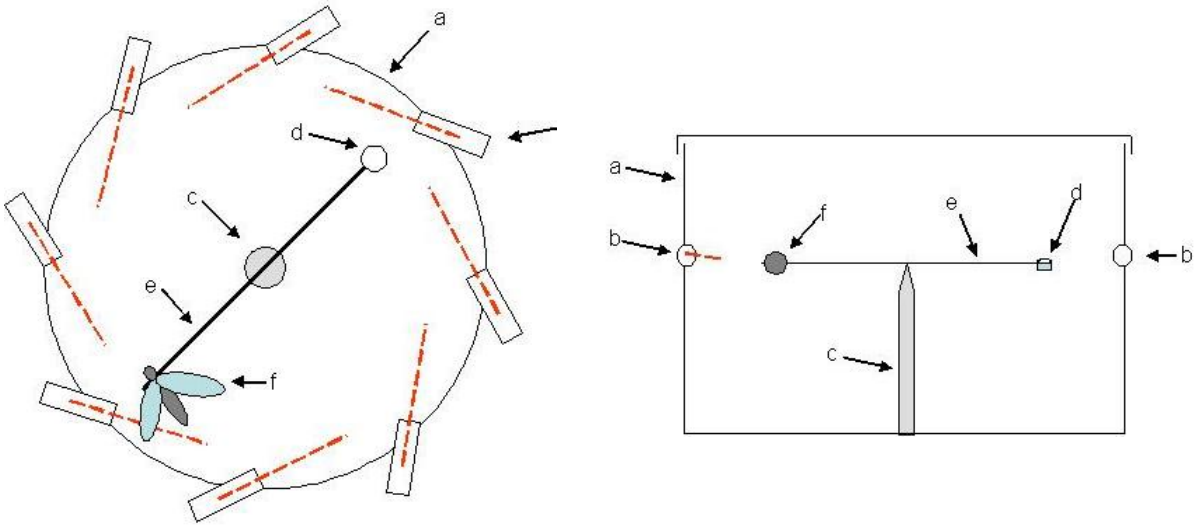

Fig. 2.2: Construction drawing of the flight chamber for flight performance tests; showing top and lateral view: a = cylindrical Plexiglass housing (diameter = 240 mm), b = multiple borings equipped with LEDs, c = central, fixed beam (length 93 mm) with needle b bearing, d = variable counterbalance on the end of the rotating beam, e = rotating beam (80 mm) with tiny magnets on both ends, f = tested individual attached via entomological needle and magnetism.

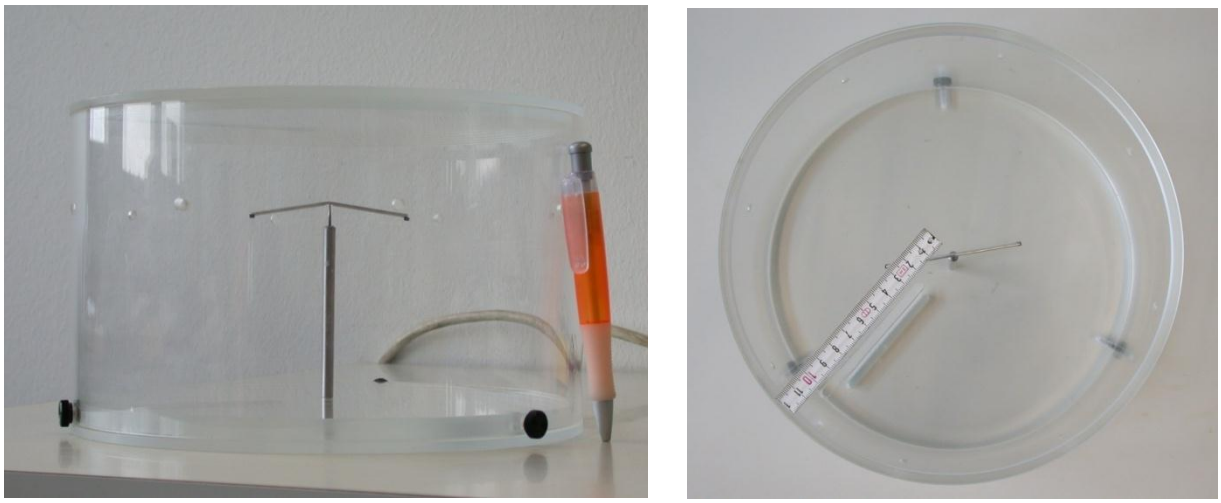

Fig. 2.3: Flight chamber for flight performance tests corresponding to the construction drawing without LED lighting; a = top view, b = lateral view.

All individuals tested were coupled to the rotating beam via a needle and a magnet. We tried two different mounting strategies with the individuals.

First, the needle was glued to the thoracotergit of the specimen with Toolcraft activator for superglue and Loctite 454 superglue. Magnets were attached to the ends of the rotating beam. To apply the glue the individual had to be immobile. We assured immobility by freezing the individual tested to immobility at -20°C (150 seconds). This process is reversible. During the immobility phase we attached the needle to the thoracotergit under a dissecting microscope. Then the individual was stored in a tube at room temperature for 20 minutes to recover from the freezing. Entomological needles attached to the opposite end of the rotating beam acted as counterweights for the mounted individual. Hence, the individual as well as the counter balance (more entomological needles) could be attached easily and reversibly. The beam is mounted freely on a needle bearing on the central column. The friction between the rotating beam and the needle bearing was below the detection limit of the spring balance (Pesola LightLine 10010).

Second, we mounted the needle to the thoracosternit, which proved very difficult. We took the legs of the immobilized specimen and glued the needle on from beneath in the same procedure as described above. Then the needle was glued to the beam to keep it attached and the individual in an upright position. The counterbalance had to be glued to the beam as well because more weight was necessary to keep the beam in balance.

Apart from the mounting system used, we tried different motivation techniques: not disturbing at all, nudging, and blowing lightly at it.

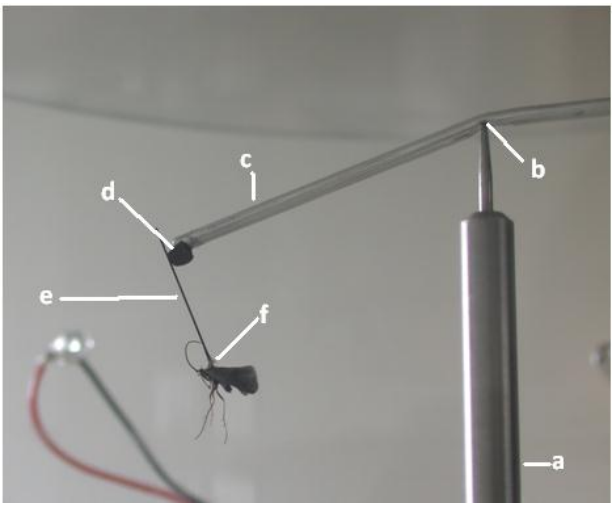

Fig. 2.4: Individual of Silo sp. installed in the flight chamber with LED lighting; a = central beam, b = needle bearing, c = free rotating collar beam, d = magnet glued to the collar beam, e = insect needle type 000, f = plastic head of the needle attached to the mesonotum.

Tab. 2.1: Synopsis of experiment set-ups tested during the flight experiments; showing: motivation = applied experiment set-up; Silo sp.: + = constant measurable flight activity, - = no measurable and constant flight activity.

Motivation	*Silo* sp.
Daylight	+
Twilight	-
Night	-
Redlight	-
increased humidity	-
Headwind	-
running light/redlight	-
Running light/twilight	-
Running light/darkness	-
without honey	-
with honey	-
Mazerat females	-
Mazerat males	-

Different experiment set-ups were tested for their influence on flight activity (Tab. 2.1). Flying animals were observed and rounds flown were counted; total flight time was measured with a stop watch. Immediately after testing individuals were preserved dryly in a tube at -20°C in a freezer awaiting biometric investigation.

2.2.4 Flight morphometric parameters

The wings of every tested specimen were disconnected from the body at the wing joints with dissection forceps, marked individually, and photographed using a binocular microscope (Olympus SZX9) and camera (moticam 2000 2.0M, produced by Motic China Group 2004). Pictures of the all the wings and the remaining body were taken as colour photos of 800 x 600 pixels resolution. Maximum possible magnification was chosen for each wing. Subsequently all colour photos were converted to 8-bit greyscale pictures using Corel Photo-Paint X5 v.15.2.0.661 (Corel Corporation, 2010).

All parameters were measured to the nearest 0.1 µm using ImagePro Analyzer 6.3 (Media Cybernetics, 2008). Most Trichoptera couple their fore- and hind-wings into a single composite aerofoil (Ivanov, 1985; Grodnitsky, 1999; Wootton, 2002). Therefore, the total width of fore and hind wing is considered wing width, while wing area is the total area of all four wings.

For the *Silo* species additional weight parameters were measured. Dryly preserved animals were defrosted at room temperature and total body mass (wet weight) as well as thorax mass were recorded with a microbalance AEG-220 by Shimadzu Corporation to the nearest of 0.01 mg. After dissection, the thorax, containing the wing muscles, was weighed and the proportion of the thorax to total weight was calculated (relative thoracic mass) (altered after Hoffsten, 2004).

The following indices were calculated to characterize wing morphology:

(1) Since body size varies considerably across species an index of relative wing length was used, which simply equals the ratio of forewing to body length (Malmqvist, 2000).
(2) AR I is a dimensionless measure of the wing shape and is calculated by dividing wing length by wing width of the fore and hind wings combined, as the fore and hind wings of caddisflies operate in flight as a single lifting surface (Grodnitsky, 1999).
(3) AR II is defined as the ratio of the wing span to its mean chord; therefore it is calculated as wing span squared divided by total wing area and is a dimensionless number (Lindhe Norberg, 2002).
(4) Sexual size dimorphism given as male-to-female wing length ratio according to Gullefors & Petersson (1993) was calculated for all applicable species.

(5) Wing loading was calculated by dividing total body mass by total wing area (Vogel, 1981).

(6) Morphological size-dependencies within one investigated group were calculated as ratios of all measured parameters based on the mean of forewing length as reference parameter.

2.2.5 Morphometric and ecological data analysis

All investigated species were assigned values on habitat specialization and stream zonation preference according to the freshwaterecology.info database (Graf & Schmidt-Kloiber, 2008). Here, a habitat specialist is defined to prefer one out of 13 habitat categories, whereas stream zonation preference is coded in a ten point assignment system which is based on the known (or estimated) average distributions, of a taxon within the environmental gradient (Graf & Schmidt-Kloiber, 2008): every 10 % occurrence in a reach equal one point in the system. These detailed categories were simplified into the broader stream zones preference and altitude preference. In both parameters adjacent regions (e.g. hypocrenal and epirhithral or submontane and colline) cumulatively exceeding 5 points were considered predominantly inhabited regions (Tab. 2.2). Adjacent regions in some categories and/or species had imbalanced occurrence values. This information was indicated by capital letters for the more frequently inhabited region. In terms of emergence/flight period the information was simply transferred in a letter coding indicating the predominant emergence season with capital letters.

Tab. 2.2: Showing the ecological information on goerid caddisflies as extracted from freshwaterecology.info (Graf & Schmidt-Kloiber, 2008).

	stream zonation preference										altitude preference								emergence/flight period				
	euc	hyc	erh	mrh	hrh	epo	mpo	hpo	lit	pro	niv	sni	alp	sal	mon	smo	col	pla	win	spr	sum	aut	
G. pilosa					5	3			2					1	1	4	4			3	6		1
S. nigricornis		3	3	2	2									1	2	4	3			2	6		2
S. pallipes		2	4	4										2	3	3	2			2	8		
S. piceus			1	3	4	2								1	3	5	1			3	7		

We used linear regression analysis to identify relationships between the morphometric parameters measured (body length, forewing length, total wing width and total wing area).

A one-way ANOVA was used to compare the means of the morphometric parameters taken. In advance we tested on departures from normality (Kolmogorov-Smirnov and Shapiro-Wilk tests) and homoscedasticity (Levene-test). Following the one-way ANOVA we used the Tukey-B post-hoc test to identify morphologically similar groups of species which differ from all other species ($p<0.05$). The Tukey-B test was conducted on all morphometric parameters analysed with the ANOVA.

These morphologically similar species and/or groups of species were displayed in a table. Then the condensed, species-specific ecological information from the freshwaterecology.info database (Graf & Schmidt-Kloiber, 2008) was added to the table with the homogenous species groups. This enabled the verification if differences in ecological requirements reflect in morphological differences. Differences between sexes of one species were tested with t-tests in all measured morphometric parameters. All analyses were conducted with SPSS 18.0 (PASW Statistics 18, 2009) except linear regression analysis for morphologic parameters (SigmaPlot 11.0; Systat Software, 2008) and calculation of coefficients of variation (Statistica 9.0; Statsoft Inc., 2009).

2.3 Results

2.3.1 Breeding of *Silo* spp. in the climate chamber

A total of 90 individuals of *Silo* spp. was collected as fifth instar larvae or pupae in the Felderbach on April 10th 2010. During the period of May 10th to June 24th 75 % of the collected individuals emerged in the laboratory; in case of *S. nigricornis* 21 females and 11 male, in *S. pallipes* 5 female and 9 male, and in case of *S. piceus* 4 female and 10 male individuals. The remaining 25 % of individuals stocked to aquaria either drowned or did not emerge at all.

2.3.2 Flight performance experiment under laboratory conditions

The first mounting strategy was performed on 95 % of the individuals tested. Only one specimen of *S. nigricornis* showed constant measurable flight performance (Tab. 2.3) in standard experiment set-up. The other tested individuals showed different reactions while being mounted in the experimental section, e.g. they tried to escape by running, flapped

their wings a few times, or displayed total immobility. The situation did not change when we took of the legs (5% of individuals tested). We tested different experimental setting as well with three individuals per setting. No constant, measureable flight performance was recorded in any other experiment set-up than the standard.

Tab. 2.3: Data on flight interval of the tested individual of *S. nigricornis*; Interval = number of flight intervals, Duration = duration of flight stage in seconds, Rounds = number of flown rounds during one flight stage, Distance = flown distance in m, Velocity = calculated mean flight velocity during the flight stage in m s^{-1}.

Interval	Duration [s]	Rounds	Distance [m]	Velocity [m s^{-1}]
1	231	154	38.70	0.17
2	17	9	2.26	0.13
3	22	16	4.02	0.18
4	11	5	1.26	0.11
5	22	3	0.75	0.03

2.3.3 Flight morphometric parameters

Altogether, we investigated 90 specimens representing 45 male and 45 female caddisflies belonging to 4 species and 2 genera of the family Goeridae. In case of *G. pilosa* a total of 15 males and 15 females per species were tested, while in the three *Silo*-species the amount of specimens per sex varied but individuals of both sexes were present (Tab. 2.4). Species differed strongly between each other. *G. pilosa* males and females exceeded all remaining species in size parameters by far but males also showed the highest variability in directly measured parameters (Tab. 2.4). Within the genus *Silo* the picture is more complicated. In the size parameters forewing length, wing width, and wing area *S. nigricornis* is the biggest species measured and *S. pallipes* males are the smallest (Tab. 2.4), except in body length. In body length *S. piceus* males are the smallest and *S. pallipes* females to the biggest (Tab. 2.4). In RWL males of *S. nigricornis* and *S. piceus* have the highest values and the females of both species have the smallest; all remaining species-sex groups are within this range (Tab. 2.5). The aerodynamic indices AR I and II the values range from *S. piceus* females with the smallest to *S. nigricornis* males with the highest values, but no clear species order is visible within this range (Tab. 2.5). Male-to-female wing ratio gives information on the proportion of forewing lengths between the sexes of the same species; *S. nigricornis* and *S. piceus* have

equally the highest value, followed by *G. pilosa* and the lowest value is in *S. pallipes* (Tab. 2.5).

Tab. 2.4: Synopsis of data on morphologic variation of adult goerid caddisflies; showing species, number of male (m) and female (f) individuals (n), forewing length (mm), total area of all wings (mm²), cumulative width of fore and hind wing (mm), and body length (mm) in arithmetic mean±95% CL and variation coefficient.

			Forewing length [mm]		Area $_{tot}$ [mm²]		Width $_{tot}$ [mm]		Body [mm]	
Species	Sex	N	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV
G. pilosa	f	15	12,26 ± 0,31	4,49	156,71 ± 4,96	5,71	9,82 ± 0,21	3,85	9,83 ± 0,85	15,57
	m	15	11,57 ± 0,41	6,45	132,86 ± 14,85	20,18	9,06 ± 0,53	10,64	8,70 ± 0,84	17,46
S. nigricornis	f	21	9,13 ± 0,12	2,99	91,88 ± 3,42	8,18	7,60 ± 0,21	5,96	8,50 ± 0,21	5,34
	m	11	9,38 ± 0,14	2,29	76,22 ± 3,98	7,77	7,00 ± 0,21	4,54	6,25 ± 0,38	9,14
S. pallipes	f	5	8,73 ± 0,37	3,43	77,52 ± 9,81	10,19	6,92 ± 0,54	6,26	8,65 ± 0,71	6,59
	m	9	7,80 ± 0,10	3,46	56,02 ± 3,20	7,42	6,01 ± 0,21	4,52	6,31 ± 0,37	7,72
S. piceus	f	4	7,81 ± 0,46	3,71	75,80 ± 3,31	2,74	6,95 ± 0,18	1,65	7,53 ± 0,33	2,78
	m	10	8,07 ± 0,13	2,18	68,42 ± 6,22	12,71	6,75 ± 0,25	5,26	5,89 ± 0,17	3,99

Tab. 2.5: Synopsis of data on morphologic variation of adult goerid caddisflies; showing species, number of male (m) and female (f) individuals (n), dimensionless indices: RWL ((forewing length) body^{-1}), AR I ((forewing length) width^{-1}), AR II (span² (total wing area)$^{-1}$) in arithmetic mean ± 95% CL, and male-to-female wing ratio (male forewing length (female forewing length)$^{-1}$).

			relative wing length	Aspect ratio I	Aspect ratio II	male/female
Species	Sex	N	mean ± 95% CI	mean ± 95% CI	mean ± 95% CI	wing length
G. pilosa	f	15	1,28 ± 0,11	1,25 ± 0,03	4,63 ± 0,16	0,94
	m	15	1,36 ± 0,10	1,28 ± 0,05	4,79 ± 0,29	
S. nigricornis	f	21	1,08 ± 0,03	1,21 ± 0,03	4,39 ± 0,15	1,03
	m	11	1,51 ± 0,08	1,34 ± 0,05	5,38 ± 0,28	
S. pallipes	f	5	1,01 ± 0,08	1,26 ± 0,06	4,78 ± 0,26	0,89
	m	9	1,24 ± 0,06	1,30 ± 0,03	5,01 ± 0,14	
S. piceus	f	4	1,04 ± 0,08	1,12 ± 0,07	3,88 ± 0,27	1,03
	m	10	1,37 ± 0,04	1,2 ± 0,04	4,44 ± 0,31	

Mass parameters in flight morphology enable a closer look into the flight capacity of species. Hence, we measured total mass and thorax mass in lab-individuals of *Silo*. The female's mass parameter included egg mass in all species as the measurements were conducted on unfertilised female. Due to this cause females of all species have a comparably high total mass and the variability is especially high in *S. piceus* (Tab. 2.6). All males were lighter than females of the same species and reached between 50% (*S. nigricornis* and *S. pallipes*) and 75% (*S. piceus*) of the female total mass (Tab. 2.6). The measurement of thorax mass is a way

to assess the flight muscle mass without high preparation effort. Female thorax mass was heavier in all cases than the male thorax mass, with *S. pallipes* females being the heaviest and *S. pallipes* males being the lightest of all (Tab. 2.6). Relative thorax mass (RTM) gives the proportion of total mass to thorax mass. Interestingly, females of all species reach a RTM of about 28-30% whereas males reach 34-38% (Tab. 2.6). Wing loading is one of many parameters considered in the topic of possible flight velocity, because it defines the amount of weight which has to be lifted per area wing. Wing loading is high in all females, but also very variable in *S. piceus* (CV=52.39) and in comparable between all species in males (Tab. 2.6).

Tab. 2.6: Synopsis of data on morphologic variation of adult goerid caddisflies; showing species, number of male (m) and female (f) individuals (n), total body mass (wet weight; mg), thorax mass (wet weight; mg), RTM (percentage of thorax of total mass), and wing loading (total weight (wing area)$^{-1}$; mg mm^{-2}) in arithmetic mean ± 95% CL.

			Mass $_{tot}$ [mg]		Thorax mass [mg]		% Thorax		wing loading [mg mm^{-2}]	
Species	Sex	N	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV
S. nigricornis	f	21	10,04 ± 0,99	21,74	2,92 ± 0,37	27,76	28,85 ± 1,52	11,55	0,11 ± 0,01	22,35
	m	11	5,55 ± 1,36	36,52	2,10 ± 0,52	36,70	37,85 ± 4,15	16,34	0,07 ± 0,02	34,56
S. pallipes	f	5	10,54 ± 2,91	22,26	3,12 ± 1,43	36,85	28,72 ± 8,60	24,11	0,14 ± 0,03	15,24
	m	9	4,84 ± 0,92	24,62	1,88 ± 0,47	32,37	38,20 ± 3,89	13,25	0,09 ± 0,02	26,25
S. piceus	f	4	8,00 ± 6,48	50,94	2,50 ± 2,31	58,15	30,91 ± 8,42	17,11	0,11 ± 0,09	52,39
	m	10	5,74 ± 1,30	31,75	2,00 ± 0,55	38,15	34,40 ± 3,78	15,38	0,08 ± 0,02	34,17

Linear regression analysis of body length, forewing length and wing area was conducted over all species and sexes as well as genus and sex specific (Tab. 2.7). In forewing length to body length the regression of females ($r^2 = 0.83$) showed a significantly higher stability index than the regression of male ($r^2 = 0.06$) values, while the regression of forewing length on body length on all species and sexes showed a poor stability index ($r^2 = 0.52$; Tab. 2.7). Sex specific regression of body length on total wing area showed only poor stability indices (Tab. 2.7).

Tab. 2.7: Regression analysis of wing morphometry of adult goerid caddisflies; showing parameters correlated, sex groups, regression equation, and stability index.

Parameters	Sex	Regression equation	Stability index (r^2)
Forewing length on body lenth	females	y = 0.23 + 1.01x	0.83
	males	y = 2.97 + 0.89x	0.06
	all	y = 2.01 + 0.61x	0.52
Wing area on body length	females	y = 139.09 - 11.74x	0.22
	males	y = 25.29 + 6.86x	0.06

In addition to the linear regression analysis we calculated size ratios within one species between each size parameters measured (Tab. 2.8). Morphological size-dependencies for wing area, wing width and body length within one investigated group (Tab. 2.8) varied between sexes of a species; *G. pilosa* exceeded all other species in RWA, but not in the remaining parameters. Then we tested these ratios on differences (Tab. 2.9). In 4 of 6 cases males of different species differed in all tested size-ratios but in females only *G. pilosa* differed from *S. nigricornis* and *S. piceus* in all size-ratios (Tab. 2.9).

Tab. 2.8: Overview on size-ratio between morphological parameters within one species-sex group based on forewing length.

Species	Sex	Length	Area tot	Width tot	Body
S. nigricornis	f	1	10,07	0,83	0,93
	m	1	8,13	0,75	0,67
S. pallipes	f	1	8,88	0,79	0,99
	m	1	7,18	0,77	0,81
S. piceus	f	1	9,71	0,89	0,96
	m	1	8,48	0,84	0,73
G. pilosa	f	1	12,78	0,80	0,80
	m	1	11,48	0,78	0,75

Tab. 2.9: Differences between size-ratio of wing area, wing width, and body length tested with t-test; showing t test results for wing area/wing width/body length, ns=not significant, *= p<0.05, **= p<0.01, *** p<0.001).

	S. nigricornis f	*S. nigricornis* m	*S. pallipes* f	*S. pallipes* m	*S. piceus* f	*S. piceus m*	*G. pilosa* f	*G. pilosa* m
S. nigricornis f	-	***/***/***	**/*/n.s.	**/n.s./***	n.s./**/n.s.	n.s./***/**	**/**/***	***/**/**
S. nigricornis m	***/***/***	-	**/**/***	**/**/***	***/***/***	n.s./***/**	***/n.s./*	***/**/**
S. pallipes f	**/*/n.s.	**/**/***	-	**/n.s./***	*/**/n.s.	**/***/**	***/n.s./***	***/**/n.s.
S. pallipes m	**/n.s./***	**/**/***	**/n.s./***	-	***/***/***	**/***/**	***/n.s./n.s.	***/*/n.s.
S. piceus f	n.s./**/n.s.	***/***/***	*/**/n.s.	***/***/***	-	*/*/***	**/**/***	**/*/*
S. piceus m	n.s./***/**	n.s./***/**	**/***/**	**/***/**	*/*/***	-	***/**/n.s.	***/*/*
G. pilosa f	**/**/***	***/n.s./*	***/n.s./***	***/n.s./n.s.	**/**/***	***/**/n.s.	-	**/n.s./n.s.
G. pilosa m	***/**/**	***/**/**	***/**/n.s.	***/*/n.s.	**/*/*	***/*/*	**/n.s./n.s.	-

The females of one species are commonly accepted as the dispersing sex. Nevertheless, the literature gives contradicting results in field experiments (Kovats et al., 1996; Sode & Wiberg-Larsen, 1993). We tested our data on sexual dimorphism in all parameters measured to answer this question on a morphological basis only. *G. pilosa* is different to the *Silo*-species in applicable parameters because males exceed females in forewing length, wing width, and wing area, but there is no difference in body length as well as all dimensionless parameters (Tab. 2.10). In the genus *Silo*, on the other hand, females exceed males in all parameters measured, except *S. nigricornis,* where the situation is vice-versa in forewing length (Tab. 2.10). In *S. piceus* the only difference in a parameter measured is in body length, the remaining values are similar (Tab. 2.10). Next to the parameters measured we tested the dimensionless and aerodynamic parameters as well. In RWL males have bigger wings than females in all species (Tab. 2.10). In AR I and II males have an advantage in distance dispersal in *S. nigricornis* and *S. piceus*, but we found no difference in *S. pallipes* (Tab. 2.10).

Tab. 2.10: Differences between sexes of means of morphologic measurements and indices tested with t-test; ns=not significant, *= p<0.05, **= p<0.01, *** p<0.001).

Species	Forewing length		Width $_{tot}$		Area $_{tot}$		Body length		Relative wing length		AR I		AR II	
S. nigricornis	m>f	*	f>m	***	f>m	***	f>m	***	m>f	***	m>f	***	m>f	***
S. pallipes	f>m	***	f>m	***	f>m	**	f>m	***	m>f	***		ns		ns
S. piceus		ns		ns		ns	f>m	***	m>f	***	m>f	*	m>f	*
G. pilosa	m>f	**	m>f	*	m>f	**		ns		ns		ns		ns

The mass parameters measured reflect dispersal capacity. The results are contradicting. In absolute measures females are heavier than males in *S. nigricornis* and *S. pallipes*, but there

is no difference in *S. piceus* in any parameter measured or calculated (Tab. 2.11). The RTM is used as a proxy for flight muscle mass, which gives a relation of the potential power applied to the aerofoils. Surprisingly, males exceed females in RTM in *S. nigricornis* and *S. pallipes* (Tab. 2.11). Wing loading, on the other hand, gives a relation of the possible flight velocity, meaning high wing loading enables faster flight (Roff, 1991). In *S. nigricornis* and *S. pallipes* females have higher wing loading than males (Tab. 2.11).

Tab. 2.11: Differences between sexes of means of morphologic measurements and indices tested with t-test; ns=not significant, *= p<0.05, **= p<0.01, *** p<0.001).

Species	Mass $_{tot}$		Mass $_{Thorax}$		Relative thorax mass		Wing loading	
S. nigricornis	f>m	***	f>m	*	m>f	***	f>m	***
S. pallipes	f>m	***	f>m	*	m>f	*	f>m	**
S. piceus		ns		ns		ns		ns

2.3.4 Morphometric and ecological data analysis

The measured and calculated parameters of all species-sex groups investigated were tested for significance using separate one-way ANOVAs for each parameter. In forewing length (F=179.29, p<0.001), total wing width (F=72.35, p<0.001), wing area (F=88.85, p<0.001) and RWL (F=18.68, p>0.001) significant differences were found. The Tukey-B post-hoc test (p<0.05) identified morphologically homogenous species-sex- groups which are similar in the parameter investigated. Then we displayed the Tukey-B-groups on the background of the ecological parameter (Fig. 2.5, 2.6, and 2.7). The species in one box are morphologically similar, but different (p<0.05) than all other boxes (Fig. 2.5, 2.6, and 2.7); the size of the box expresses the stream region (Fig. 2.5), altitudinal belt (Fig. 2.6), and emergence period (Fig. 2.7) of all species named in the box. Interestingly, individuals of *G. pilosa* are always different from any other morphologically similar group (Fig. 2.5, 2.6, and 2.7). The results show that the genus *Silo* is concentrated in the hypocrenal to hyporhithral region, is spread over a variety of altitudes, and has long emergence periods (Fig. 2.5, 2.6, and 2.7).

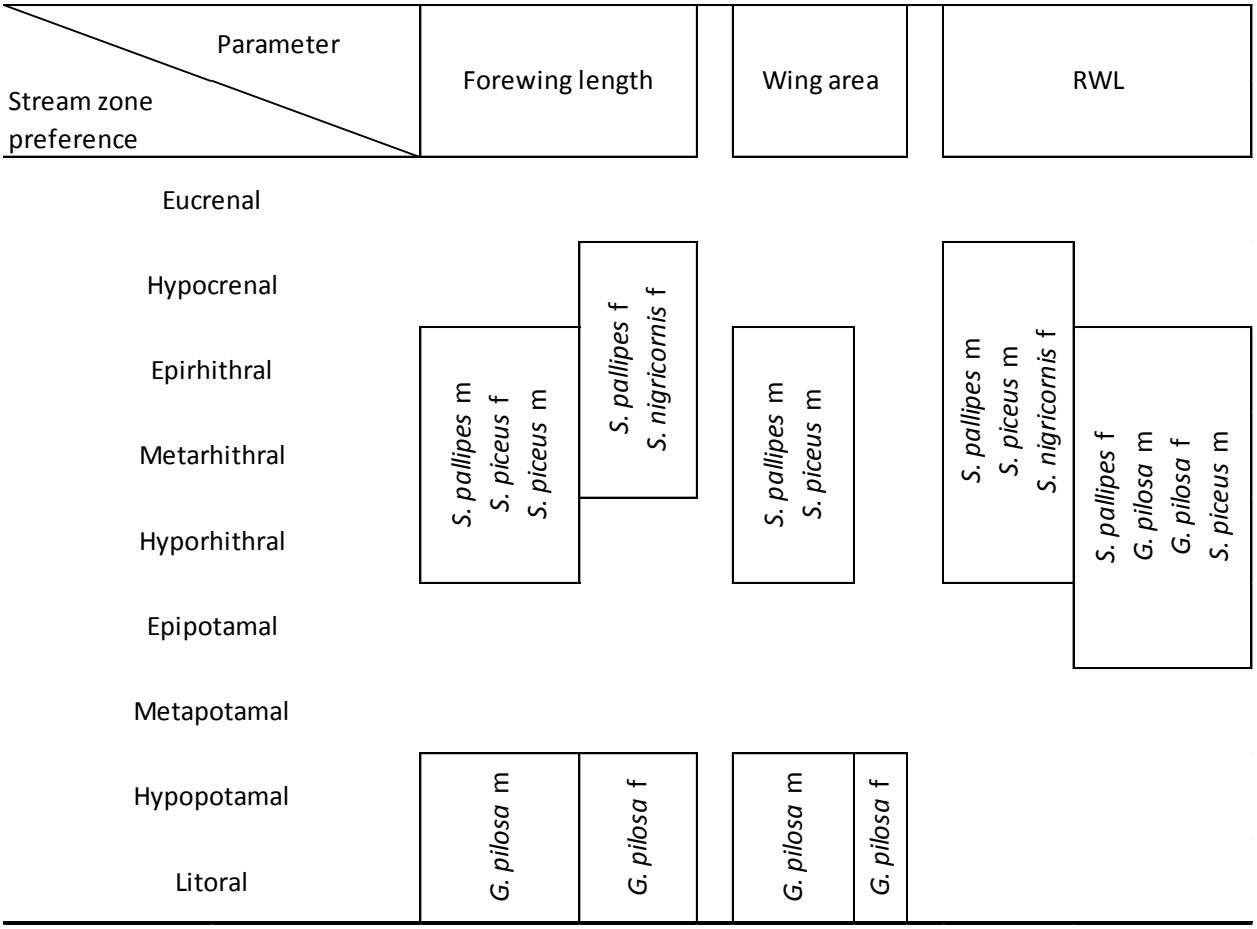

Fig. 2.5: Synopsis of Tukey-B post-hoc test ($p<0.05$) between significantly different species groups with associated ecology traits based on forewing length, RWL and wing area; showing species, sex, and stream zonation preference.

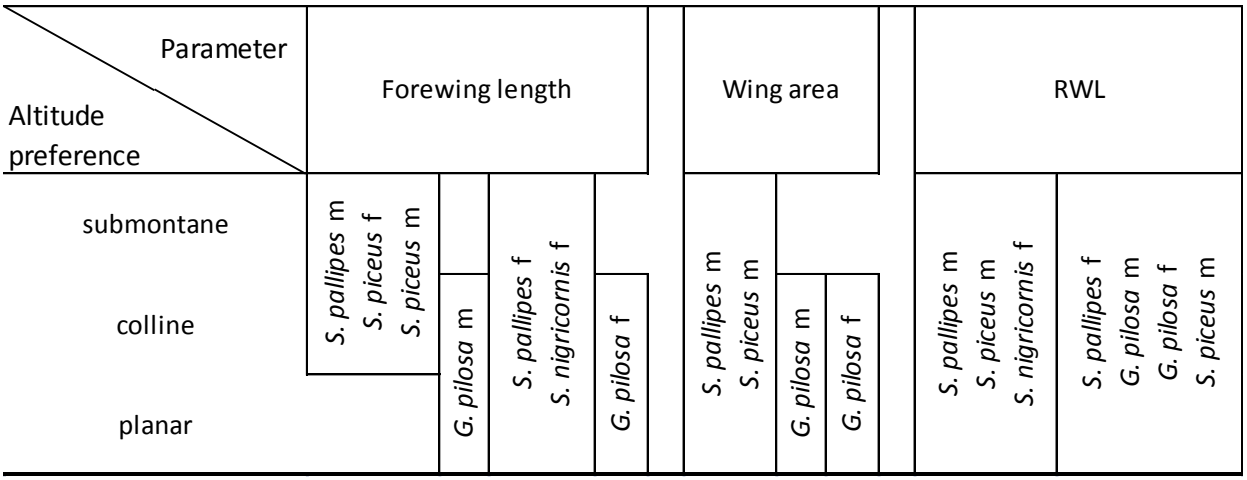

Fig. 2.6: Synopsis of Tukey-B post-hoc test ($p<0.05$) between significantly different species groups with associated ecology traits based on forewing length, RWL and wing area; showing species, sex, and altitudinal belt preference.

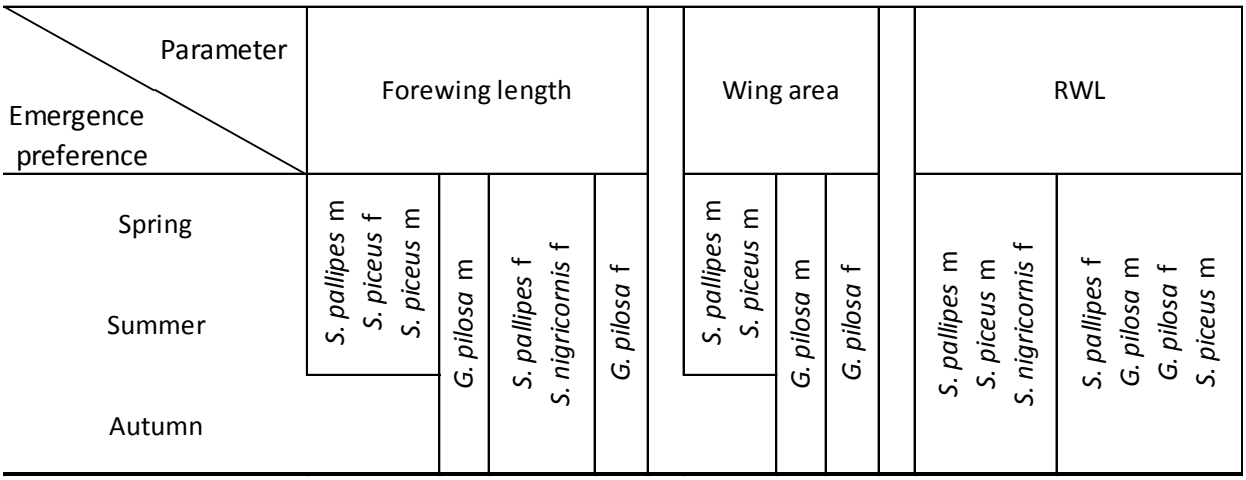

Fig. 2.7: Synopsis of Tukey-B post-hoc test ($p<0.05$) between significantly different species groups with associated ecology traits based on forewing length, RWL and wing area; showing species, sex, and emergence period.

2.4 Discussion

Merolimnic insects in the adult stage must find suitable larval habitats for survival and/or further dispersal of their population. The dispersal ability manifests in different scales: morphology defines the flight ability itself and the behaviour defines the percentage of dispersing individuals (male or female). We measured flight morphological parameters and compared size-independent aerodynamic indices to test if differences in the blueprint can be determined and allocated to species-specific ecological requirements.

We acquired a detailed species-sex specific wing-morphology and mass parameter database and tested for possible morphological blueprints and similarities upon different taxonomy levels. On genus-level the blueprints in measured parameters and RWL are different between *Goera* and *Silo*, which supports the current taxonomy. The variability in both genera is quite low. All individuals tested originate from two systems only, all *Silo*-specimens were collected at the Felderbach and all *G. pilosa* individuals are from the Fulda. Therefore this variability is to be considered natural. We found a medium strong relationship between forewing length and body length ($r^2=0.52$; all groups). The total number of tested males and females was equal but group size was unequal. This relationship casts doubt on the common use of forewing length for identification of the size of a species as used in Malicky (2004) and Goretti et al. (2005). Apart from directly measured parameters, we calculated a series of

dimensionless indices. We found no differences in the indices and we believe this to be a consequence of the low individual numbers tested, especially in the females.

No genera comparison was possible in weight parameters; *Silo*-species only were bred in the lab. Within *Silo* we found no differences in any weight parameter measured or calculated and believe this to be due to the small sample size.

We tested the species blueprint on sexual dimorphism in two approaches. First we tested the size-ratios based on forewing length between sexes and species. Male blueprints do differ between species in most cases in all parameters considered. In *S. nigricornis* and *S. piceus* blueprints are different in all parameters tested, in *S. pallipes* two out of three parameters differ, and in *G. pilosa* the ratio to wing area only is different.

Apart from the ratios, we tested the directly measured and calculated parameters on sexual dimorphism. Sexual dimorphism in measured parameters is genus-specific. In *Silo* females exceed males in most cases. Forewing length in *S. nigricornis* is an exception to this pattern as males have longer forewings than females. In *S. piceus* females are bigger than males in body length only. In the dimensionless indices the picture is different. In all cases males exceed females. In the weight parameters, *S. piceus* is similar in sexes, but in *S. nigricornis* and *S. pallipes* females exceed males in all parameters other than RTM. We conclude, that aerodynamic indices and RTM suggest males as the dispersing sex in *Silo*. The relationship in forewing length on body length supports this because the relationship in *Silo* males (r^2=0.06) was barely existent. Therefore, the forewings in males are different, but body length is similar. As a consequence wing-morphometry only suggests different dispersal strategies in the males: *S. nigricornis* and *S. pallipes* have an advantage in distance dispersal if compared to *S. piceus*.

We conducted a flight-experiment to quantify the distance travelled actively (flight) by the individual adult caddisfly. The selection of the genus *Silo* based on three arguments. First, *Silo* is easy to handle in the lab, we reached 60 % successful emergence. Second, our sampling area was easy to reach, near to the lab, well studied, and it houses all three *Silo*-species known for Germany. Third, Ehlert (2009) reported vectored and persistent mass-flights of *S. nigricornis* at the sampling site. Unfortunately, one specimen only out of 60 tested showed a constant, measurable flight performance. Therefore, we are positive that the flight chamber itself works properly and probably repeatable. Following criteria would

have to be considered before conducting another test with the flight chamber. First, the flight chamber is limited to medium sized caddisflies in the chosen dimension. If used for smaller species, the rotating beam has to be shortened and the friction of the bearing should be minimised. As a consequence the additional weight transported by the specimen would decrease. If used for bigger species, the bearing of the rotating beam should be secured. The "successful" candidate nearly dismounted the rotating beam. We would suggest a fixed, rotating bearing. As a consequence to the failure of the flight-experiment, we use the mass data to analyse the question of flight ability.

Variation in flight muscle mass, in this study assessed via RTM, is an obvious example of a polymorphism that affects flight ability (Harrison, 1980; Dingle, 1996; Hoffsten, 2004). Marden (2000) gives 12 to 16 % of their total mass as critical flight muscle mass and states that flight performance will increase with the increase of this percentage. Hoffsten (2004) suggested a thorax size above 30% represents a critical minimum for thorax mass for caddisflies adapted to dispersal flight. The critical minimum must therefore be applied on females with fecundated eggs. No egg deposition took place in our experiments because all individuals were kept separately at all times. In *S. nigricornis* and *S. pallipes* males the RTM was well above the critical minimum and significantly higher than in the corresponding females (28.7-30.9%). This suggests males as the dispersing sex in *Silo*. On the other hand, large body mass, in combination with high wing loading, typically indicates fast flight (Roff, 1991). This enables a flying insect to escape drag forces operating at low Reynolds numbers (Re), which for small insects makes it 'relatively more difficult to get anywhere' (Vogel, 1981). Therefore, high speed and large body mass are more energy efficient, reducing costs per unit distance (Eckert et al., 1988). In females of *S. nigricornis* and *S. pallipes* wing loading is significantly higher than in the males contradicting the results from RTM.

The final hypothesis was that the morphology resembles the preferred altitude, stream zone and emergence period of the larvae. Next to the current velocity preferences (Bacher, 1995), stream insect larvae often prefer a specific altitude, e.g. submontane, colline, or planar. We used the Tukey-B post-hoc test to identify morphologically similar species-sex groups. We found, that *G. pilosa* is different in all ecological parameters considered and this is resembled in the measured parameters, but no differentiation between genera is possible in RWL. The *Silo*-species overlap in their stream zone and altitude preference and emergence period. We found that species resembling *S. piceus*-morphology should occur in higher

elevated rhithral areas, whereas species resembling the morphology of *S. nigricornis* and *S. pallipes* should prefer crenal to rhithral stream zones in lower elevations. Still, all species resemble medium-sized adult caddisflies, are closely related, have quite similar ecological requirements, and can be found at the sampling site. In addition, König & Waringer (2008) proved an extraordinarily high drift resistance in *S. nigricornis* larvae. All this proposes that the majority of *Silo* spp.-specimen try to stay close to their larval habitats and that only a small to very small (1 out of 60!) proportion of individuals will disperse at all. Along with the morphological ability to disperse goes a behavioural aspect. Not every individual of one population will disperse. Weather conditions like rain, wind, and cloud amount may influence the dispersal of populations. Sode & Wiberg-Larsen (1993) explained a mid-season dip in flight activity of *S. pallipes* with relatively low mean air temperature and high mean wind speed. Waringer (1991) tested the influence of precipitation, wind speed and night air temperature on light trap catching success of Trichoptera. Only the effect of air temperature was correlated with flight activity (Waringer, 1991). As well has wind a strong effect on the flight direction of Trichoptera in that the adults generally fly against the wind (Usseglio-Polatera, 1987). Sode & Wiberg-Larsen (1993) contradict this result with increased abundance of *S. pallipes* in wind direction.

In conclusion, aerodynamic considerations and observations of dispersal indicate a causal link between morphological factors and dispersal ability. Nevertheless those parameters are not sufficient to explain the observed dispersal behaviour as was proved in the experiment conducted. Therefore, a new focus should be put on behavioural analysis to identify parameters which trigger dispersal as no definitive morphological cause can be named.

3. Flight-morphology of Central European Trichoptera (Insecta) in relation to their ecological preferences and flight behaviour

3.1 Introduction

Caddisflies (Insecta: Trichoptera) are diverse and abundant in most freshwater habitats (Hoffsten, 2004) and more than 1000 species are described for Europe (Malicky, 2005). The egg, larval and pupal stages are mainly aquatic, while the adults live in the terrestrial environment (Graf et al., 2008). The adults are generally considered strong fliers because most species are fully winged, and many of them display intricate swarming flights (Johnson, 1969; Gullefors & Petersson, 1993). The primary purpose of the adult phase of the typical aquatic insect life cycle is mating and the deposition of eggs in habitats suitable for larval development (Kovats et al., 1996).

Trichoptera occur in a wide range of different habitats. Species may prefer lentic or lotic current regimes, different times for emergence, and various meeting patterns for successful pair formation and mating. While some species tolerate a wide range of ecological conditions, others are much more specific (Graf et al., 2008).

The life-cycle of Trichoptera requires various functions of the morphology. This morphology changes in evolutionary processes. Hence, information on the size and shape of the body in animal populations, namely in an order of insects, allows to observe how much the body model of different species can change within a determinate systematic group (Goretti et al., 2005). This approach also makes it possible to identify morphometric variations (Cadrin, 2000) within an order of insects, which may be linked to the species- or genus- or family-specific ecological needs of the species given.

Numerous biometric studies have been conducted on a population or a community of lentic and lotic freshwater invertebrates (e.g. Smock, 1980; Meyer, 1989; Wenzel et al, 1990; Rasmussen, 1993; Robertson, 1995; Dudgeon, 1996; Grubaugh et al, 1997; Fonseca & Esteves, 2000). However, morphometric studies of all the taxa of a faunal group (namely of an order of insects) distributed over large geographical areas are rarely found in literature (Goretti et al., 2005).

It can be easily observed experimentally that the morphological model for adult caddisflies is certainly less differentiated than that of larval specimens (Goretti et al., 2005). In Trichoptera one general blueprint seems to fit all investigated species as stated in Goretti et al. (2005).

As a consequence, we address the following hypothesises on the basis of newly gained flight-morphological data for 86 German Trichoptera species. Additionally, we take ecological and behavioural data into account and establish links between morphology and current preference, emergence period, and flight behaviour.

First, size proportions within one species are specific and differ significantly from one genus/family to another because the body blueprint is a mirror to evolutional development lines.

Second, sexual dimorphism is present in all species, as females are designed to carry and deposit eggs whereas males are not required to transport the additional load in their adult stage. Hence, the aerodynamical design of females is more energy-efficient than in males.

Third, we investigate if emergence duration reflects in morphology. Only if individuals of both sexes meet, successful mating is possible. Strategies for meeting involve a very strict timing of emergence in short-lived animals as seen e.g. in Ephemeroptera, but longer-living animals with no such strict timing need mobility. Hence, species with a long emergence period will have a flight-morphology suitable for vagility.

Fourth, swarming is one strategy for pair formation and we test if different pair formation strategies are reflected in morphology. It involves hovering in the air and mating behaviour in Trichoptera is spread along a gradient from very simple to quite complex. Increasingly complex mating behaviour requires the ability to hover in the air (Gullefors & Petersson, 1993).

Last, water bodies differ in their current regime; running waters (lotic) are connected, whereas standing water bodies (lentic) are more isolated. Species inhabiting lentic environments require strategies to compensate the possible loss of a whole population. Consequently these species have a greater urge to disperse than lotic species. Hence, lentic species will have a morphology adapted to dispersal.

3.2 Methods

We investigated the wing morphology of adult caddisflies from the collections of Thomas Ehlert (2009), Wolfram Graf, Daniel Hering, Armin Lorenz, Thomas Pitsch and Peter Rolauffs originating from different parts of Germany and Austria. The regional provenance of the collections of Ehlert, Pitsch and Rolauffs is stated in detail in Chapter 1. The collection of Daniel Hering was sampled mainly during the years from 1990 to 1996 from the large rivers of central and southern Germany as for example the Neckar (48° 2′ N, 8° 31′ O), Lahn (50° 53′ N, 8° 14′ O) and Isar (48° 48' N, 12° 58′ O). Individuals originating from the collection of Armin Lorenz were sampled in 2001 at the Eder (51° 13′ N, 9° 27′ O). The collectors used a variety of methods, including light trapping, emergence traps, sweep-netting and hand-picking. All specimens were identified to the species-level and sex and preserved in minimum 70 % ethanol until dissection.

Altogether, we investigated 2317 specimens representing 1161 male and 1144 female caddisflies belonging to 86 species, 42 genera and 16 families of caddisflies. In 60 cases a total of 15 males and 15 females per species were tested, in 17 cases the number of specimens was lower but individuals of both sexes were present whereas in 9 cases only specimen of one sex were investigated (Tab.3.1 & 3.2).

The preparation and dissection of specimen followed a standardised routine. First all wings of one individual were dissected with dissecting forceps, placed on a slide and photographed through a binocular microscope (Olympus SZX9) using a digital camera (moticam 2000 2.0M, produced by Motic China Group 2004). The body was embedded in plasticine and as well photographed. Photographs of all body parts were taken at maximum possible magnification as colour photos of 800 x 600 pixels resolution. Serial photos were taken of body parts which exceeded the picture at minimum magnification as for e.g. in *Odontocerum albicorne* (Odontoceridae). In these cases the serial pictures were stitched together with the photo stitching software PTGui Pro v8.3 (New House Internet Services B.V., Rotterdam, The Netherlands, 2009) and therefore exceeded the size of 800 to 600 pixels afterwards. Subsequently all colour photos were converted to 8-bit greyscale pictures using Corel Photo-Paint X5 v.15.2.0.661 (Corel Corporation, 2010).

Wing length, width and area as well as body length and span between wing joints were measured to the nearest 0.1 µm using ImagePro Analyzer 6.3 (Media Cybernetics, 2008). Most Trichoptera couple their fore and hind wings into a single composite aerofoil (Ivanov, 1985;

Grodnitsky, 1999; Wootton, 2002). Therefore, wing width is the total of fore and hind wing width, while wing area is the total area of all four wings. Minor damaged wings were reworked individually during the measurement process. Majorly damaged or missing wings were replaced by the arithmetic mean of the remaining parameter specific values of all measured specimens belonging to the investigated species and sex. In total 288 of 32 975 measurements were replaced which equal approximately 0.9 % of the total.

The following indices were calculated to characterize wing morphology and were already introduced in chapter 2. Additionally we calculated the relative wing area (6):

(1) Since body size varies considerably across species an index of RWL was used, which simply equals the ratio of forewing to body length (Malmqvist, 2000).
(2) AR I is a dimensionless measure of the wing shape and is calculated by dividing wing length by wing width of the fore and hind wings combined, as the fore and hind wings of caddisflies operate in flight as a single lifting surface (Grodnitsky, 1999).
(3) AR II is defined as the ratio of the wing span to its mean chord; therefore it is calculated as wing span squared divided by total wing area and is a dimensionless number (Lindhe Norberg, 2002).
(4) Sexual size dimorphism given as male-to-female wing length ratio according to Gullefors & Petersson (1993) was calculated for all applicable species.
(5) Wing loading was calculated by dividing total body mass by total wing area (Vogel, 1981).
(6) The relative wing area (RWA) is the ratio of the forewing length to the total wing area of one species; it gives information on the relation of the individual to its wing area.

Few linear body dimensions (wing length, wing width and body length) were analyzed by linear regression with SigmaPlot 11.0 (Systat Software, 2008). The descriptive investigation of morphometry excluded all limnephilid species. This is a commonly used measure to describe the stability of biometric size ratios on the level of the order.

On the species level we tested for sexual dimorphism in all directly measure parameters and indices calculated with t-tests ($p<0.05$) using SPSS for Windows 18.0 (PASW Statistics 18, 2009).

After log-transformation of the directly measured parameters a Principal Component Analysis (PCA) was used to study the multidimensional morphological relationships and aerodynamics in the order. This analysis was conducted with the data-set including all limnephilid species. The

analysis was performed by the means of CANOCO 4.51 (Biometrics Plant Research, Wageningen 1999-2003). Various shapes as overlays for the PCA result were constructed using SigmaPlot 11.0. Firstly, the taxonomic family information was applied on the shape. Secondly, the results RWA-index were split into thirds and assigned “small” for the lower third, “medium” for the medium third, and “high” for the upper third of the values; this information was transferred to a shape. Based on species specific ecological information extracted from the freshwaterecology.info database (Graf & Schmidt-Kloiber, 2008), shape overlays for the PCA result were constructed for the emergence period (long, short) and current regime. The information on current regime is divided into seven categories in the database, three of which specify lotic preference (rheo to limnophil, rheophil, and rheobiont), three specify lentic preferences (limno to rheophil, limnophil, and limnobiont), and one for indifferent to current regime. We simplified the information to three categories: lentic, lotic, and indifferent. Last, we collected species-specific information on flight behaviour from the literature and personal communication with Wolfram Graf which results build an overlay with four categories: swarming, not swarming, night active, and no information. The division swarming and not swarming does not implicate that all species considered are solely day active as e.g. *L. basale* is active day and night. The definition of swarming used is any kind of hovering flight with little or no distance flight regardless the sex or number of individuals present in the air. This flight behaviour is believed to have impact on the mating chances of individuals. Not swarming adds all other flight movements with clear gain of distance. Night active animals are likely to use pheromones for pair formation; therefore no hovering for visual detection is necessary.

3.3 Results

3.3.1 Biometric parameters

Material for the analysis of biometric parameters excluded individuals belonging to the family Limnephilidae as their biometry is discussed in detail in Chapter 1. Hence, the material investigated for biometric analysis contains 1632 specimens representing 936 male and 800 female adult Trichoptera belonging to 60 species, 29 genera and 14 families.

Families display a wide variation of morphometric measurements, ranging from very small wing lengths (3-5 mm) in i.e. *Hydroptila* (Hydroptilidae), *Adicella* (Leptoceridae), and *Lype* (Psychomyiidae) to rather larger forewings (10-15 mm) in *Plectrocnemia* (Polycentropodidae),

and *Sericostoma* (Sericostomatidae), up to *Odontocerum* (Odontoceridae) which bear by far the largest forewings (15-21 mm; Tab. 3.1 & 3.2). The morphometric blueprint within one genus is quite affixed as seen in for example *Athripsodes* (Leptoceridae) or *Rhyacophila* (Rhyacophilidae; Tab. 3.1 & 3.2). An exception to this pattern are the genera *Ceraclea* and *Oecetis* (both Leptoceridae) which varies in forewing length from 5.5-12.3 mm in *Ceraclea* and 5.4-12.8 mm in *Oecetis* and in wing area from 29.2-109.4 mm² in *Ceraclea* and in *Oecetis* from 22.2-110.6 m² and is therefore quite variable (Tab. 3.1 & 3.2). Also in wing area one can find affixed sizes within one genus as e.g. in the small *Agapetus* (14-32 mm²; Glossosomatidae), medium sized *Silo* (66-91 mm²; Goeridae), as well as in the big *Philopotamus* (101-172 mm²; Philopotamidae; Tab. 3.1 & 3.2). Contradicting, *Oecetis* and *Ceraclea* species show an enormous variation in wing area, ranging from 22 to 110 mm² and 29 to 109 mm², respectively (Tab. 3.1 & 3.2). The variation within one species and sex for directly measured parameters is given as coefficient of variation. In wing length, wing width and body length the majority of species-sex groups show only little variation as e.g. in *Athripsodes* (4.1-13.5) and *Philopotamus* (3.4-11.1). *M. nigra* (5.4-48.7; Leptoceridae) on the other hand show a wide variation within species-sex groups as well as *O. albicorne* (7.8-46.3; Tab. 3.1 & 3.2).

Tab. 3.1: Synopsis of data on morphologic variation of adult caddisflies; showing species, number of male (m) and female (f) individuals (n), wing length (mm), forewing length as in Malicky (2004), cumulative width of fore and hind wing (mm), total area of all wings (mm²), and body length (mm) in arithmetic mean±95% CL and variation coefficient.

			Wing length		FWL	Wing area		Wing width		Body	
Species	Sex	n	mean ± 95% CI	CV	Malicky	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV
Brachycentridae											
Micrasema longulum	m	15	5.70 ± 0.22	7.2	5-6	30.86 ± 2.78	16.3	4.60 ± 0.64	25.4	5.08 ± 0.22	8.1
McLACHLAN, 1876	f	15	5.55 ± 0.53	17.4	7	38.15 ± 1.81	8.6	6.14 ± 0.78	22.9	4.42 ± 0.17	7.0
Micrasema setiferum	m	15	5.15 ± 0.10	3.8	5-6	21.91 ± 0.96	7.9	3.36 ± 0.11	6.2	3.75 ± 0.12	5.9
(PICTET, 1834)	f	15	5.26 ± 0.20	6.9	5-7	21.20 ± 1.76	15.0	3.39 ± 0.19	10.6	3.94 ± 0.40	18.6
Ecnomidae											
Ecnomus tenellus	m	15	5.03 ± 0.16	5.9	4-6	18.49 ± 1.09	10.7	2.89 ± 0.12	8.0	4.41 ± 0.22	9.3
(RAMBUR, 1842)	f	15	5.68 ± 0.19	6.1	5-6	22.56 ± 1.67	13.4	3.10 ± 0.15	8.8	4.70 ± 0.29	11.3
Glossosomatidae											
Agapetus delicatulus	m	15	4.58 ± 0.13	5.4	5-6	16.09 ± 0.80	9.0	2.76 ± 0.07	4.6	3.91 ± 0.17	8.0
McLACHLAN, 1884	f	15	6.52 ± 0.61	16.9	5-6	32.32 ± 4.04	22.6	3.75 ± 0.19	9.4	4.37 ± 0.58	24.3
Agapetus fuscipes	m	15	4.28 ± 0.15	6.4	3-5	14.33 ± 0.86	10.9	2.59 ± 0.06	4.5	3.50 ± 0.12	6.6
CURTIS, 1834	f	15	4.53 ± 0.17	7.1	3-5	15.54 ± 1.47	17.1	2.67 ± 0.18	12.5	4.02 ± 0.19	8.9
Agapetus ochripes	m	15	4.96 ± 0.13	4.8	3-4	20.5 ± 0.84	7.5	3.25 ± 0.09	5.0	3.71 ± 0.2	10.0
CURTIS, 1834	f	15	5.07 ± 0.11	4.1	4-5	19.96 ± 0.87	7.9	3.12 ± 0.12	7.4	4.00 ± 0.19	8.6
Glossosoma boltoni	m				6-9						
(CURTIS, 1834)	f	15	8.12 ± 0.28	6.3	7-9	53.32 ± 3.59	12.2	5.30 ± 0.15	5.2	7.99 ± 0.56	12.8
Glossosoma conformis	m	3	8.16 ± 0.97	4.8	7-8	57.68 ± 8.20	5.7	5.87 ± 0.48	3.3	8.14 ± 1.78	8.8
(NEBOISS, 1963)	f	15	9.56 ± 0.22	4.2	7-9	74.06 ± 3.47	8.5	6.20 ± 0.17	5.1	9.36 ± 0.38	7.5
Goeridae											
Goera pilosa	m	15	11.56 ± 0.41	6.4	8-10	132.86 ± 14.84	20.2	9.06 ± 0.53	10.6	8.69 ± 0.84	17.5
(FABRICIUS, 1775)	f	15	12.26 ± 0.30	4.5	9-11	156.70 ± 4.95	5.7	9.82 ± 0.20	3.8	9.82 ± 0.84	15.6
Silo nigricornis	m	15	9.34 ± 0.13	2.5	6-11	76.58 ± 3.08	7.3	7.05 ± 0.16	4.3	6.31 ± 0.30	8.7
(PICTET, 1834)	f	15	9.13 ± 0.15	3.1	7-12	91.96 ± 4.16	8.2	7.60 ± 0.25	6.2	8.48 ± 0.25	5.4
Silo pallipes	m	15	7.60 ± 0.18	4.4	6-9	53.58 ± 2.52	8.5	5.86 ± 0.15	4.8	6.14 ± 0.25	7.4
(FABRICIUS, 1781)	f	15	8.89 ± 0.29	6.1	6-10	76.93 ± 6.09	14.3	6.82 ± 0.34	9.0	8.91 ± 0.57	11.7
Silo piceus	m	15	8.01 ± 0.10	2.4	6-10	66.87 ± 4.14	11.2	6.71 ± 0.16	4.4	5.82 ± 0.14	4.5
BRAUER, 1857	f	15	8.00 ± 0.35	8.1	6-10	72.39 ± 2.54	6.4	6.81 ± 0.16	4.3	7.21 ± 0.24	6.2
Hydropsychidae											
Cheumatopsyche lepida	m	15	5.83 ± 0.25	7.8	5-.5	27.22 ± 2.27	15.1	3.82 ± 0.16	7.7	4.38 ± 0.30	12.6
(PICTET, 1834)	f	15	5.50 ± 0.53	17.6	-	35.52 ± 1.93	9.8	5.63 ± 0.80	25.9	5.06 ± 0.26	9.3
Hydropsyche angustipennis	m	15	8.44 ± 0.53	11.4	8-10	66.85 ± 8.65	23.4	6.09 ± 0.39	11.7	7.44 ± 0.44	10.7
(CURTIS, 1834)	f	15	10.38 ± 0.98	17.1	-	95.19 ± 16.20	30.9	7.04 ± 0.62	15.9	8.59 ± 0.57	12.1
Hydropsyche pellucidula	m	15	12.67 ± 0.43	6.2	9-14	143.44 ± 8.77	11.0	9.36 ± 0.31	6.1	9.56 ± 0.48	9.1
(CURTIS, 1834)	f	15	13.4 ± 0.26	3.5	-	157.60 ± 5.39	6.2	9.44 ± 0.20	3.9	10.66 ± 0.36	6.2
Hydropsyche saxonica	m	15	10.89 ± 0.23	4.0	11-13	128.03 ± 7.14	10.1	8.93 ± 0.26	5.4	9.97 ± 0.50	9.2
(McLACHLAN, 1884)	f	13	12.88 ± 0.25	3.3	-	133.05 ± 8.52	10.6	8.57 ± 0.40	7.8	10.18 ± 0.59	9.7
Hydropsyche siltalai	m	15	11.81 ± 0.43	6.7	10-12	119.99 ± 8.24	12.4	8.57 ± 0.39	8.4	10.48 ± 0.55	9.5
DÖHLER, 1963	f	15	10.38 ± 0.34	5.9	-	103.30 ± 6.51	11.4	7.56 ± 0.24	5.9	10.21 ± 0.43	7.7
Hydroptilidae											
Allotrichia pallicornis	m	15	5.17 ± 0.18	6.4	4-5	15.45 ± 0.92	10.8	2.61 ± 0.13	9.1	3.25 ± 0.10	6.1
(EATON, 1873)	f	15	5.30 ± 0.20	7.0	4	14.73 ± 0.71	8.8	2.40 ± 0.10	7.7	3.79 ± 0.15	7.4
Hydroptila forcipata	m	15	3.19 ± 0.09	5.4	3-4	5.71 ± 0.39	12.5	1.54 ± 0.17	19.9	2.07 ± 0.13	11.7
(EATON, 1873)	f	15	3.61 ± 0.20	10.3	-	7.46 ± 0.97	23.6	1.90 ± 0.21	20.3	3.24 ± 0.12	6.7
Hydroptila sparsa	m	15	3.13 ± 0.21	12.5	2.5-3	5.29 ± 0.56	19.3	1.54 ± 0.11	13.8	2.69 ± 0.19	12.9
(CURTIS, 1834)	f	15	3.09 ± 0.14	8.3	-	5.81 ± 0.61	19.0	1.51 ± 0.09	10.9	3.13 ± 0.14	8.3
Ithytrichia lamellaris	m	15	3.43 ± 0.09	5.1	3-3.5	6.34 ± 0.33	9.6	1.63 ± 0.09	10.3	2.54 ± 0.20	14.7
(EATON, 1873)	f	15	3.33 ± 0.10	5.7	3-3.5	5.94 ± 0.44	13.6	1.53 ± 0.15	18.0	2.81 ± 0.17	11.0
Lepidostomatidae											
Lepidostoma basale	m	15	10.03 ± 0.28	5.2	8-10	73.48 ± 3.62	8.9	5.82 ± 0.18	5.8	8.25 ± 0.49	10.8
(KOLENATI, 1848)	f	15	10.34 ± 0.41	7.3	8-10	75.42 ± 7.50	18.0	5.77 ± 0.34	10.9	5.45 ± 0.26	8.7
Lepidostoma hirtum	m	15	9.28 ± 0.30	5.9	6-9	73.15 ± 3.68	9.1	6.24 ± 0.19	5.6	7.28 ± 0.35	8.8
(FABRICIUS, 1775)	f	15	10.68 ± 0.44	7.6	6-9	90.9 ± 5.33	10.6	6.79 ± 0.22	5.9	5.89 ± 0.18	5.7

One method to study the affixation of biometric relationships at level of the order Trichoptera is linear regression analysis. Wing length and wing width (r^2=0.76) as well as wing length and body length (0.78) show a strong relationship when all species groups are considered (Fig. 3.1). Additionally, we calculated the regressions sex-specific: in wing length on wing width the relationship for males ($y=0.37 + 0.66x$; $r^2 = 0.82$) is stronger than in females ($y = 0.88 + 0.59x$; $r^2 = 0.75$) and in wing length on body length the relationship in females ($y = 1.38 + 0.68x$; $r^2 = 0.78$) is stronger than in males ($y = 1.92 + 0.63x$; $r^2 = 0.76$).

3.2: Synopsis of data on morphologic variation of adult caddisflies; showing species, number of male (m) and female (f) individuals (n), wing length (mm), forewing length as in Malicky (2004), cumulative width of fore and hind wing (mm), total area of all wings (mm²), and body length (mm) in arithmetic mean±95% CL and variation coefficient.

			Wing length		FWL	Wing area		Wing width		Body	
Species	Sex	n	mean ± 95% CI	CV	Malicky	mean ± 95% CI	CV	mean ± 95% CI	CV	mean ± 95% CI	CV
Leptoceridae											
Adicella reducta	m	15	3.77 ± 0.18	8.9	5-7	25.86 ± 1.97	13.8	5.44 ± 0.26	8.7	7.36 ± 0.25	6.2
(McLACHLAN, 1865)	f	15	3.86 ± 0.35	16.7	5.5-7	27.49 ± 2.92	19.2	5.65 ± 0.38	12.3	5.71 ± 0.23	7.3
Athripsodes albifrons	m	15	8.29 ± 0.34	7.6	7-9	65.95 ± 5.14	14.1	6.02 ± 0.25	7.8	6.56 ± 0.29	8.0
(LINNAEUS, 1758)	f	15	7.51 ± 0.24	5.9	6-8	51.93 ± 3.84	13.4	5.19 ± 0.25	8.9	6.37 ± 0.30	8.7
Athripsodes bilineatus	m	14	8.1 ± 0.32	7.0	7-9	60.68 ± 5.40	15.4	5.95 ± 0.29	8.5	6.71 ± 0.39	10.1
(LINNAEUS, 1758)	f	14	7.49 ± 0.30	7.0	6-10	52.46 ± 4.40	14.5	5.27 ± 0.24	7.9	6.89 ± 0.53	13.5
Athripsodes cinereus	m	15	10.32 ± 0.25	4.4	9-11	89.09 ± 3.52	7.2	7.11 ± 0.16	4.1	7.91 ± 0.33	7.5
(CURTIS, 1834)	f	15	9.62 ± 0.27	5.2	8-10	74.62 ± 4.71	11.4	6.26 ± 0.27	7.8	7.41 ± 0.30	7.3
Ceraclea albimacula	m	9	11.43 ± 1.74	19.9	11-12	109.36 ± 12.64	15.0	8.62 ± 0.33	5.1	7.64 ± 1.51	25.9
(RAMBUR, 1877)	f	15	9.38 ± 1.48	28.6	10-12	87.19 ± 9.95	20.6	7.78 ± 0.60	13.9	7.11 ± 0.53	13.7
Ceraclea annulicornis	m	15	10.55 ± 0.58	10.0	9-11	100.94 ± 10.77	19.3	7.96 ± 0.44	10.0	7.11 ± 0.37	9.6
(STEPHENS, 1836)	f	15	6.72 ± 0.21	5.8	8-9	52.64 ± 4.61	15.8	5.46 ± 0.28	9.3	6.45 ± 0.20	5.8
Ceraclea dissimilis	m	15	8.18 ± 0.24	5.4	8-9	65.40 ± 5.22	14.4	6.31 ± 0.31	8.9	6.64 ± 0.25	7.0
(STEPHENS, 1836)	f	15	4.65 ± 0.18	7.0	6-8	44.42 ± 3.26	13.3	7.36 ± 0.27	6.6	6.18 ± 0.26	7.9
Ceraclea fulva	m										
(RAMBUR, 1842)	f	15	5.83 ± 0.52	16.3	11-12	29.19 ± 2.80	17.4	4.28 ± 0.76	32.3	5.12 ± 0.36	12.8
Ceraclea nigronervosa	m	15	12.27 ± 0.6	8.9	10-13	101.83 ± 7.91	14.0	7.72 ± 0.31	7.4	9.01 ± 0.39	7.9
(RETZIUS, 1783)	f										
Mystacides azurea	m	15	8.03 ± 0.20	4.7	6-7	55.49 ± 3.06	10.0	5.41 ± 0.22	7.4	7.15 ± 0.25	6.3
(LINNAEUS, 1761)	f	15	7.49 ± 0.31	7.7	6-7	45.59 ± 2.93	11.6	4.72 ± 0.19	7.5	6.90 ± 0.42	11.2
Mystacides longicornis	m	15	7.27 ± 0.45	11.3	7-9	39.05 ± 3.88	18.0	4.54 ± 0.22	8.8	8.75 ± 0.54	11.2
(LINNAEUS, 1758)	f	15	6.97 ± 0.57	15.0	7-9	35.21 ± 4.56	23.4	4.15 ± 0.35	15.3	8.08 ± 1.34	29.9
Mystacides nigra	m	15	6.48 ± 1.56	43.7	7	49.30 ± 7.18	26.3	6.99 ± 0.59	15.3	6.43 ± 0.19	5.4
(LINNAEUS, 1758)	f	9	8.62 ± 0.37	5.7	7	52.05 ± 4.98	12.5	5.17 ± 0.32	8.2	8.25 ± 0.88	14.0
Oecetis lacustris	m	3	5.41 ± 0.42	3.2	6-7	22.22 ± 2.70	4.9	3.12 ± 0.56	7.2	5.13 ± 0.50	4.0
(PICTET, 1834)	f	15	7.28 ± 0.35	8.9	6-8	33.24 ± 3.51	19.1	3.72 ± 0.24	11.8	5.57 ± 0.42	13.7
Oecetis notata	m	4	6.05 ± 0.23	2.4	7-8	27.74 ± 3.45	7.8	3.76 ± 0.34	5.8	5.72 ± 0.37	4.2
(RAMBUR, 1842)	f	6	5.94 ± 0.40	6.5	7-8	25.60 ± 3.63	13.5	3.49 ± 0.50	13.7	6.17 ± 0.52	8.0
Oecetis ochracea	m	15	12.59 ± 0.24	3.5	10-13	107.65 ± 4.96	8.3	7.13 ± 0.28	7.1	8.99 ± 0.34	7.0
(CURTIS, 1825)	f	15	12.76 ± 0.52	7.4	9-10	110.62 ± 8.20	13.4	7.30 ± 0.37	9.4	8.75 ± 0.40	8.3
Molannidae											
Molanna angustata	m	15	12.52 ± 0.23	3.3	9-12	135.32 ± 4.35	5.8	7.45 ± 0.12	3.1	10.87 ± 0.20	3.4
(CURTIS, 1834)											
Odontoceridae											
Odontocerum albicorne	m	15	15.41 ± 2.43	28.5	12-16	212.70 ± 48.86	41.5	11.82 ± 0.84	12.9	11.01 ± 0.47	7.8
(SCOPOLI, 1763)	f	15	21.12 ± 3.24	27.8	14-19	322.84 ± 82.72	46.3	12.92 ± 1.38	19.3	12.84 ± 1.31	18.6
Philopotamidae											
Philopotamus ludificatus	m	15	10.77 ± 0.31	5.3	9-13	144.58 ± 4.92	6.2	8.13 ± 0.11	2.5	8.10 ± 0.33	7.4
(McLACHLAN, 1878)	f	15	12.25 ± 0.36	5.4	10-13	172.30 ± 13.78	14.4	8.84 ± 0.36	7.4	9.24 ± 0.50	9.9
Philopotamus montanus	m	15	9.89 ± 0.18	3.4	8-13	101.57 ± 3.06	5.4	7.44 ± 0.12	3.1	10.05 ± 0.45	8.1
(DONOVAN, 1813)	f	15	11.33 ± 0.40	6.4	9-13	124.76 ± 7.26	10.5	8.01 ± 0.22	5.1	10.13 ± 0.62	11.1
Wormaldia occipitalis	m	15	4.45 ± 0.30	12.4	6-7	51.71 ± 2.86	10.0	7.08 ± 0.35	9.1	8.01 ± 0.57	12.9
(PICTET, 1834)	f	15	4.45 ± 0.13	5.3	-	54.42 ± 3.19	10.6	7.41 ± 0.26	6.4	8.70 ± 0.32	6.7
Polycentropodidae											
Cyrnus trimaculatus	m	15	6.31 ± 0.27	7.9	5-6	32.66 ± 2.14	11.8	4.06 ± 0.09	4.2	4.35 ± 0.23	9.8
(CURTIS, 1834)	f	15	7.49 ± 0.31	7.7	5-6	44.65 ± 3.60	14.6	4.62 ± 0.18	7.3	5.28 ± 0.21	7.2
Plectrocnemia conspersa	m	15	12.13 ± 0.21	3.2	9-15	131.88 ± 3.10	4.3	8.88 ± 0.14	3.0	8.79 ± 0.90	18.7
(CURTIS, 1834)	f	15	12.46 ± 1.20	17.5	9-15	157.96 ± 19.32	22.1	9.69 ± 0.43	8.1	10.65 ± 0.70	12.0
Polycentropus flavomaculatus	m	15	6.51 ± 0.20	6.8	6-9	38.45 ± 2.34	13.1	4.37 ± 0.15	7.6	5.66 ± 0.17	6.6
(PICTET, 1834)	f	15	8.24 ± 0.47	10.3	8-10	59.71 ± 7.64	23.1	5.35 ± 0.39	13.4	6.69 ± 0.30	8.2
Polycentropus irroratus	m	15	9.38 ± 0.32	6.3	4-9	71.60 ± 4.10	10.3	6.18 ± 0.15	4.5	7.10 ± 0.36	9.4
(CURTIS, 1835)	f	15	10.78 ± 0.87	14.6	9-10	106.25 ± 9.51	16.2	7.68 ± 0.17	4.1	6.91 ± 0.26	6.9
Psychomyiidae											
Lype phaeopa	m	14	3.99 ± 0.29	12.9	4-6	16.31 ± 1.40	15.0	2.71 ± 0.12	7.7	3.49 ± 0.44	22.1
(STEPHENS, 1836)	f	9	4.98 ± 0.30	8.0	4-6	21.88 ± 2.26	13.5	3.05 ± 0.16	6.9	4.53 ± 0.37	10.7
Lype reducta	m	15	2.96 ± 0.14	9.1	4-6	15.18 ± 1.12	13.4	4.02 ± 0.16	7.6	5.42 ± 0.24	8.2
(HAGEN, 1868)	f	15	4.78 ± 0.62	23.5	-	22.81 ± 2.55	20.2	3.81 ± 0.56	26.9	4.74 ± 0.23	9.0
Psychomyia pusilla	m	15	5.40 ± 0.17	5.9	3-4	18.60 ± 1.21	11.8	2.56 ± 0.10	7.6	4.08 ± 0.15	6.8
(FABRICIUS, 1781)	f	15	5.95 ± 0.19	6.0	3-4	21.31 ± 1.42	12.1	2.60 ± 0.07	5.1	4.95 ± 0.26	9.7
Tinodes waeneri	m	15	6.99 ± 0.24	6.3	5-10	35.15 ± 2.54	13.1	3.90 ± 0.15	7.3	6.31 ± 0.33	9.6
(LINNAEUS, 1758)	f	15	7.18 ± 0.54	13.8	5-8	39.28 ± 4.14	19.0	4.35 ± 0.37	15.5	6.56 ± 0.56	15.5
Rhyacophilidae											
Rhyacophila dorsalis	m	15	13.46 ± 0.46	7.6	10-12	164.01 ± 8.57	11.5	8.83 ± 0.24	6.2	11.31 ± 0.49	9.6
(CURTIS, 1834)	f	9	13.16 ± 0.89	8.8	11-14	157.8 ± 13.84	11.4	8.77 ± 0.34	5.1	11.31 ± 1.26	14.5
Rhyacophila fasciata	m	15	12.35 ± 0.25	3.8	10-14	152.25 ± 6.05	7.2	8.80 ± 0.19	4.1	9.42 ± 1.41	27.0
(HAGEN, 1859)	f	15	12.15 ± 0.2	3.1	11-14	150.13 ± 5.06	6.1	8.88 ± 0.16	3.3	9.49 ± 0.28	5.4
Rhyacophila nubila	m	14	12.00 ± 0.34	5.0	10-12	129.52 ± 7.91	10.6	7.85 ± 0.22	4.9	10.00 ± 0.41	7.2
(ZETTERSTEDT, 1840)	f	15	12.83 ± 0.39	5.7	11-14	151.07 ± 8.70	10.8	8.55 ± 0.21	4.7	10.99 ± 0.36	6.2
Rhyacophila obliterata	m	15	12.67 ± 0.41	5.9	11-13	163.19 ± 11.21	12.4	9.13 ± 0.31	6.2	9.98 ± 0.35	6.5
(MCLACHLAN, 1863)	f	5	10.85 ± 0.60	4.5	11	112.23 ± 15.99	11.5	7.12 ± 0.52	5.9	9.28 ± 0.60	5.2
Rhyacophila praemorsa	m	14	12.61 ± 0.26	3.6	11-13	135.55 ± 6.25	8.0	8.25 ± 0.20	4.4	10.68 ± 0.79	12.8
(MCLACHLAN, 1879)	f	5	11.32 ± 1.08	7.7	11-13	113.96 ± 13.72	9.7	7.36 ± 0.46	5.1	10.47 ± 0.98	7.6
Rhyacophila tristis	m	15	7.70 ± 0.30	7.1	7-10	68.54 ± 4.68	12.3	5.77 ± 0.19	6.0	7.54 ± 0.32	7.7
(PICTET, 1834)	f	5	8.62 ± 0.37	3.5	7-10	67.29 ± 7.72	9.2	5.73 ± 0.39	5.6	9.10 ± 0.61	5.4
Sericostomatidae											
Oecismus monedula	m	10	12.07 ± 0.52	6.1	10-11	107.68 ± 12.34	16.0	7.24 ± 0.47	9.1	9.19 ± 0.72	11.1
(HAGEN, 1859)	f	5	13.90 ± 0.73	4.3	12-13	144.58 ± 12.83	7.1	8.12 ± 0.52	5.2	10.88 ± 1.29	9.6
Sericostoma flavicorne	m	15	10.47 ± 0.26	4.6	10-14	87.52 ± 4.59	9.5	6.87 ± 0.23	6.2	10.78 ± 0.21	3.6
(KOLENATI 1848)	f	15	11.91 ± 0.32	4.9	-	107.89 ± 6.32	10.6	7.54 ± 0.30	7.4	10.63 ± 0.40	6.8
Sericostoma personatum	m	15	11.82 ± 0.33	5.1	8-15	121.18 ± 10.01	14.9	7.61 ± 0.42	10.0	10.45 ± 0.50	8.7
(SPENCE in KIRBY & SPENCE, 1826)	f	15	13.56 ± 0.49	6.7	10-17	135.73 ± 10.16	13.5	8.00 ± 0.50	11.4	10.39 ± 0.75	13.1

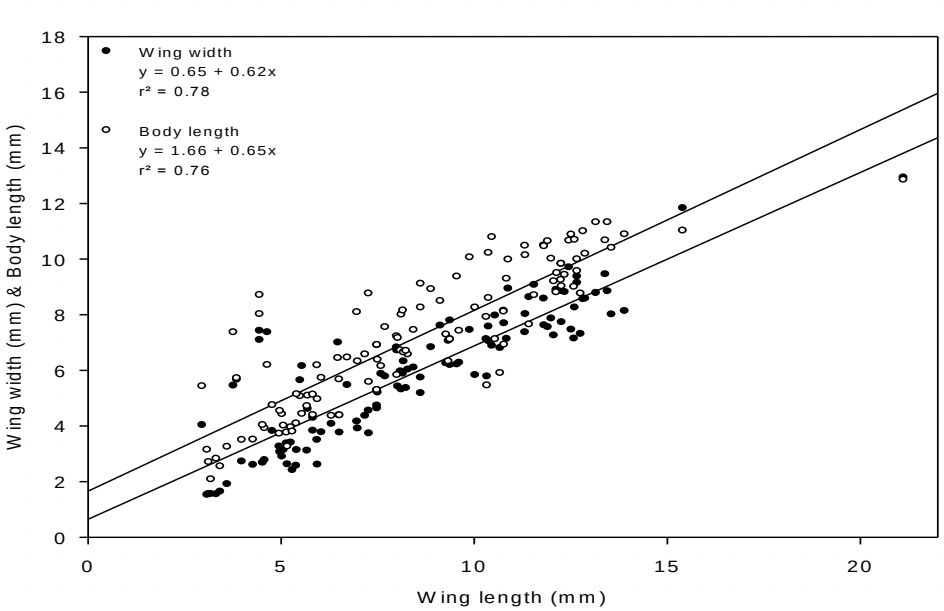

Fig. 3.1: Relationship between body length, forewing length and total width. Each circle gives a mean value for the male or the female of a species. Filled circles represent data on wing width; unfilled circles represent data on body length. Linear regression analysis indicated that the slopes of the relationships are similar.

Additionally, we calculated a number of dimensionless ratios. Variation in the RWL, a size independent measure of wing length, is wide and ranges from 0.51 in *W. occipitalis* (Philopotamidae) females to 1.45 in *O. ochracea* (Leptoceridae) females (Tab. 3.3 & 3.4). The AR I and II are a measure for distance flight efficiency; the lower limit of range in AR I is in *C. dissimilis* females (0.63; Leptoceridae), whereas *P. pusilla* females (2.27; Psychomyiidae) are the upper limit (Tab. 3.3 & 3.4). In AR II *I. lamellaris* females (8.82, Hydroptilidae) is the upper range limit whereas the lower limit is *Wormaldia occipitalis* females (1.92, Philopotamidae; Tab. 3.3 & 3.4). The male-to-female-wing ratio is an indicator to mating behaviour. We found the upper limit in *C. annulicornis* (1.57; Leptoceridae) and the lower limit in *L. reducta* (0.61; Psychomyiidae) (Tab. 3.4). The RWA is an indicator on flight behaviour; we found a wide variation in RWA ranging from 1.69 in *H. sparsa* males to 14.00 in *P. ludificatus* females (Tab. 3.3 & 3.4).

Tab. 3.3: Synopsis of data on morphologic variation of adult caddisflies; showing species, number of male (m) and female (f) individuals (n), dimensionless indices: RWL ((forewing length) body^{-1}), AR I ((forewing length) width^{-1}), AR II (span² (total wing area)$^{-1}$) in arithmetic mean, and male-to-female wing ratio (male forewing length (female forewing length)$^{-1}$), RWL (total wing area (forewing length)$^{-1}$); collection information: number of individuals collected by: P=Pitsch, R=Rolauffs, E=Ehlert, L=Lorenz, H=Hering, and G=Graf).

Species	Sex	n	Relative wing length	Aspect ratio I	Aspect ratio II	Male/female wing ratio	Relative wing area	Specimen P	R	E	L	H	G
Brachycentridae													
M. longulum	m	15	1.11	1.23	5.01	1.02	5.41			15			
	f	15	1.25	0.9	3.86		6.87			15			
M. setiferum	m	15	1.37	1.53	5.81	0.97	4.25				15		
	f	15	1.33	1.55	6.36		4.03				15		
Ecnomidae													
E. tenellus	m	15	1.14	1.74	6.53	0.88	3.67	15					
	f	15	1.2	1.83	6.8		3.97	15					
Glossosomatidae													
A. delicatulus	m	15	1.17	1.65	6.32	0.7	3.51			15			
	f	15	1.49	1.74	6.28		4.95	15					
A. fuscipes	m	15	1.21	1.64	6.33	0.94	3.34	15					
	f	15	1.12	1.69	6.56		3.43	15					
A. ochripes	m	15	1.33	1.52	5.87	0.97	4.13	15					
	f	15	1.26	1.62	6.33		3.93	15					
G. boltoni	m		1.01	1.52	5.96								
	f	15	1	1.39	5.61	0.85	6.56						15
G. conformis	m	3	1.02	1.53	5.87		7.06						3
	f	15					7.74						15
Goeridae													
G. pilosa	m	15	1.32	1.27	4.68	0.94	11.40	11	1	3			
	f	15	1.24	1.24	4.61		12.70	11	2	2			
S. nigricornis	m	15	1.48	1.32	5.31	1.02	8.19			15			
	f	15	1.07	1.2	4.33		10.00			15			
S. pallipes	m	15	1.23	1.29	5.03	0.85	7.05			15			
	f	15	0.99	1.3	4.91		8.65			15			
S. piceus	m	15	1.37	1.19	4.43	1	8.34	15					
	f	15	1.11	1.17	4.19		9.04	6		9			
Hydropsychidae													
C. lepida	m	15	1.32	1.52	5.75	1.05	4.66	15					
	f	15	1.08	0.97	4.21		6.45	15					
H. angustipennis	m	15	1.13	1.38	5.1	0.81	7.92	15					
	f	15	1.2	1.47	5.37		9.17	15					
H. pellucidula	m	15	1.32	1.35	5.25	0.94	11.30			15			
	f	15	1.25	1.41	5.37		11.70	15					
H. saxonica	m	15	1.09	1.21	4.53	0.84	11.70			11		4	
	f	13	1.26	1.5	5.89		10.30					13	
H. siltalai	m	15	1.12	1.37	5.61	1.13	10.10			15			
	f	15	1.01	1.37	5.12		9.95			15			
Hydroptilidae													
A. pallicornis	m	15	1.58	1.98	8.02	0.97	2.98				15		
	f	15	1.4	2.2	8.85		2.77				15		
H. forcipata	m	15	1.53	2.06	8.57	0.88	1.78				15		
	f	15	1.11	1.9	8.55		2.06				15		
H. sparsa	m	15	1.16	2.03	8.67	1	1.69		15				
	f	15	0.98	2.05	7.85		1.88				15		
I. lamellaris	m	15	1.34	2.1	8.73	1.03	1.84				15		
	f	15	1.18	2.17	8.82		1.78				15		
Lepidostomatidae													
L. basale	m	15	1.21	1.72	6.39	0.97	7.32	15					
	f	15	1.89	1.79	6.54		7.29	15					
L. hirtum	m	15	1.27	1.48	5.37	0.86	7.88	6		9			
	f	15	1.81	1.57	5.98		8.51	15					

Tab. 3.4: Synopsis of data on morphologic variation of adult caddisflies; showing species, number of male (m) and female (f) individuals (n), dimensionless indices: RWL ((forewing length) body^{-1}), AR I ((forewing length) width^{-1}), AR II (span² (total wing area)$^{-1}$) in arithmetic mean, and male-to-female wing ratio (male forewing length (female forewing length)-1), RWA (total wing area (forewing length)$^{-1}$); collection information: number of individuals collected by: P=Pitsch, R=Rolauffs, E=Ehlert, L=Lorenz, H=Hering, and G=Graf).

			Relative	Aspect	Aspect	Male/female	Relative	Specimen				
Species	Sex	n	wing length	ratio I	ratio II	wing ratio	wing area	P	R	E	L	H	G
Leptoceridae													
A. reducta	m	15	0.51	0.69	2.82	0.97	6.85			14		1	
	f	15	0.67	0.68	2.75		7.12			4		11	
A. albifrons	m	15	1.26	1.37	4.85	1.1	7.95	15					
	f	15	1.17	1.44	5.11		6.91	15					
A. bilineatus	m	14	1.2	1.36	5.3	1.08	7.49			14			
	f	14	1.08	1.41	5.01		7.00			14			
A. cinereus	m	15	1.3	1.44	5.51	1.07	8.63	15					
	f	15	1.29	1.53	5.75		7.75	15					
C. albimacula	m	9	1.49	1.32	5.61	1.21	9.56		9				
	f	15	1.32	1.2	4.83		9.29		15				
C. annulicornis	m	15	1.48	1.32	5.22	1.57	9.56	15					
	f	15	1.04	1.22	4.2		7.83	15					
C. dissimilis	m	15	1.23	1.29	4.68	1.76	7.99	15					
	f	15	0.75	0.63	2.77		9.55	15					
C. fulva	m												
	f	15	1.13	1.36	5.76		5.00		15				
C. nigronervosa	m	15	1.36	1.58	6.81		8.29	15					
	f												
M. azurea	m	15	1.12	1.48	5.44	1.07	6.91	15					
	f	15	1.08	1.58	5.77		6.08	15					
M. longicornis	m	15	0.82	1.6	6.31	1.04	5.37	15					
	f	15	0.86	1.67	6.42		5.05	15					
M. nigra	m	15	1	0.92	4.09	0.75	7.60	9		3		3	
	f	9	1.04	1.66	6.69		6.03			1		8	
O. lacustris	m	3	1.05	1.73	6.23	0.74	4.10	2	1				
	f	15	1.3	1.95	7.39		4.56					15	
O. notata	m	4	1.05	1.6	6.36	1.01	4.58		4				
	f	6	0.96	1.69	6.63		4.30					6	
O. ochracea	m	15	1.4	1.76	6.71	0.98	8.55	15					
	f	15	1.45	1.74	6.72		8.66	15					
Molannidae													
M. angustata	m	15	1.15	1.67	5.75		10.80	15					
Odontoceridae													
O. albicorne	m	15	1.4	1.3	5.18	0.72	13.80	15					
	f	15	1.64	1.63	6.29		15.20	15					
Philopotamidae													
P. ludificatus	m	15	1.33	1.32	3.77	0.88	13.40	15					
	f	15	1.32	1.38	4.09		14.00	15					
P. montanus	m	15	0.98	1.32	4.7	0.87	10.20			15			
	f	15	1.11	1.41	4.9		11.00					15	
W. occipitalis	m	15	0.55	0.62	1.99	1	11.60	15					
	f	15	0.51	0.6	1.92		12.20	15					
Polycentropodidae													
C. trimaculatus	m	15	1.44	1.55	5.77	0.84	5.17			15			
	f	15	1.41	1.62	5.99		5.96			15			
P. conspersa	m	15	1.37	1.36	5.3	0.97	10.80	15					
	f	15	1.16	1.28	4.69		12.60	3		12			
P. flavomaculatus	m	15	1.15	1.49	5.72	0.79	5.90	12		3			
	f	15	1.23	1.54	5.6		7.24	15					
P. irroratus	m	15	1.31	1.51	5.67	0.86	7.63	12		3			
	f	15	1.56	1.4	5.34		9.85			15			
Psychomyiidae													
L. phaeopa	m	14	1.14	1.46	5.22	0.8	4.08			14			
	f	9	1.09	1.62	5.99		4.39			9			
L. reducta	m	15	0.54	0.73	3.06	0.61	5.12			15			
	f	15	1	1.25	5.32		4.77			15			
P. pusilla	m	15	1.32	2.1	7.29	0.9	3.44	15					
	f	15	1.19	2.27	7.6		3.58	15					
T. waeneri	m	15	1.1	1.79	6.51	0.97	5.02	15					
	f	15	1.09	1.65	6.5		5.47			9		6	
Rhyacophilidae													
R. dorsalis	m	15	1.19	1.52	5.1	1.02	12.10	15					
	f	9	1.16	1.49	5.07		11.90	9					
R. fasciata	m	15	1.31	1.4	4.71	1.01	12.30	15					
	f	15	1.28	1.36	4.57		12.30	15					
R. nubila	m	14	1.19	1.52	5.31	0.93	10.70	14					
	f	15	1.16	1.5	5.16		11.70	15					
R. obliterata	m	15	1.26	1.38	4.62	1.16	12.80	15					
	f	5	1.17	1.52	5.05		10.30					15	
R. praemorsa	m	14	1.18	1.52	4.82	1.11	10.70					15	
	f	5	1.08	1.53	4.92		10.00					15	
R. tristis	m	15	1.02	1.33	4.2	0.89	8.90	15					
	f	5	0.94	1.5	5.29		7.80	5					
Sericostomatidae													
O. monedula	m	10	1.31	1.66	6.45	0.86	8.92	10					
	f	5	1.28	1.72	6.44		10.40	5					
S. flavicorne	m	15	0.97	1.52	6.05	0.87	8.35			15			
	f	15	1.12	1.58	6.29		9.05			15			
S. personatum	m	15	1.13	1.55	5.61	0.87	10.20	8		2		5	
	f	15	1.3	1.69	6.45		10.00		8			7	

Sexual dimorphism is species specific. In 31 of 60 species forewings of females are longer than in males, whereas in 10 cases male forewing exceeded females, and no difference was found in 19 cases (Tab. 3.5). No difference in any species was found in Brachycentridae, whereas in Odontoceridae and Sericostomatidae all cases were different (Tab. 3.5). The 10 cases when male exceed female forewings was found in only four families: Goeridae, Hydropsychidae, Leptoceridae, and Rhyacophilidae (Tab. 3.5). In wing area the picture is only little different. In 18 of 60 cases belonging to 9 families there is no difference, in the families of Hydropsychidae, Leptoceridae, and Rhyacophilidae are a total of 10 cases where male wing area exceeds female wing area, and in the remaining 32 cases which distribute over all families female wing area is bigger than in males (Tab. 3.5). When wing with is considered, the picture changes a little. Male wing width is bigger than female in 11 of 60 cases belonging to the families of Hydroptilidae, Hydropsychidae, Leptoceridae, and Rhyacophilidae, whereas in 27 of 60 cases belonging to 12 families females exceed males, and the remaining 22 cases (12 families) show no difference at all (Tab. 3.5). Interestingly, only in the family Polycentropodidae females have wider wing than males in all species tested (Tab. 3.5). Body length is strongly related to all other length measurement in a trichopteran body; nevertheless there is a certain amount of variability. In 9 of 60 cases belonging to the families Brachycentridae, Lepidostomatidae, Leptoceridae, Psychomyiidae, and Rhyacophilidae males are bigger than females, whereas in 29 cases belonging to 11 families the situation is vice-versa; in 22 of 60 cases there is no difference at all (Tab. 3.5). One size-independent measure of wing length is the RWL which enables the comparison of morphometry. Interestingly, in 20 of 60 cases belonging to ten families males have a higher RWL than females, but in the three families Goeridae, Hydroptilidae, and Rhyacophilidae all males exceed females (8 of 20 cases; Tab. 3.5). No difference can be found in 21 cases belonging to 11 families and in 19 cases females have a higher RWL than males, where in the families of Brachycentridae, Ecnomidae, and Lepidostomatidae all females exceed the males (4 cases; Tab. 3.5).The aerodynamic indices AR I and II are female biased in both parameters (29, respectively 21 of 60 cases); nevertheless, next to a huge number of no difference (25, respectively 30 cases) males exceed females in 6, respectively 9 of 60 cases (Tab. 3.5). Generally, the families Leptoceridae and Rhyacophilidae are male biased in most tested parameters, but only in Ecnomidae (one species *E. tenellus*) and Odontoceridae (one species *O. albicorne*) females exceed males in all parameters with differences; all remaining families display a mixture of differences (Tab. 3.5).

Tab. 3.5: Differences between sexes of means of morphologic measurements and indices tested with t-test; ns=not significant, *= p<0.05, **= p<0.01, *** p<0.001). When males exceed females (p<0.05) the field is shaded grey.

Species	Wing length		Wing area		Wing width		Body length		Relative wing length		Aspect ratio I		Aspect ratio II	
Brachycentridae														
M. longulum		n.s.	f>m	***	f>m	**	m>f	***	f>m	***	m>f	*	m>f	*
M. setiferum		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	f>m	***
Ecnomidae														
E. tenellus	f>m	***	f>m	***	f>m	*		n.s.	f>m	***	f>m	*	f>m	*
Glossosomatidae														
A. delicatulus	f>m	***	f>m	***	f>m	***		n.s.	f>m	*		n.s.		n.s.
A. fuscipes	f>m	*		n.s.		n.s.	f>m	***		n.s.		n.s.		n.s.
A. ochripes		n.s.		n.s.		n.s.	f>m	*	m>f	*	f>m	**	f>m	**
G. conformis	f>m	***	f>m	***		n.s.	f>m	*	f>m	**	f>m	***		n.s.
Goeridae														
G. pilosa	f>m	**	f>m	**	f>m	**		n.s.		n.s.		n.s.		n.s.
S. nigricornis	m>f	*	f>m	***	f>m	***	f>m	***	m>f	***	m>f	***	m>f	***
S. pallipes	f>m	***	f>m	***	f>m	***	f>m	***	m>f	***		n.s.		n.s.
S. piceus		n.s.	f>m	*		n.s.	f>m	***	m>f	***		n.s.		n.s.
Hydropsychidae														
C. lepida		n.s.	f>m	***	f>m	***	f>m	**	m>f	**	m>f	**	m>f	**
H. pellucidula	f>m	**	f>m	**		n.s.	f>m	***		n.s.	f>m	***		n.s.
H. saxonica	f>m	***		n.s.		n.s.		n.s.	f>m	***	f>m	***	f>m	***
H. siltalai	m>f	***	m>f	**	m>f	***		n.s.	m>f	***		n.s.	m>f	**
H. angustipennis	f>m	***	f>m	**	f>m	**	f>m	**	f>m	*	f>m	**		n.s.
Hydroptilidae														
A. pallicornis		n.s.		n.s.		n.s.	f>m	***		n.s.		n.s.		n.s.
H. forcipata		n.s.		n.s.	m>f	*	f>m	***	m>f	***	f>m	**	f>m	*
H. sparsa	f>m	***	f>m	**	f>m	**	f>m	***	m>f	**		n.s.		n.s.
I. lamellaris		n.s.		n.s.		n.s.	f>m	*	m>f	**		n.s.		n.s.
Lepidostomatidae														
L. basale		n.s.		n.s.		n.s.	m>f	***	f>m	***	f>m	*		n.s.
L. hirtum	f>m	***	f>m	***	f>m	***	m>f	***	f>m	***	f>m	**	f>m	***
Leptoceridae														
A. reducta		n.s.		n.s.		n.s.	m>f	***	f>m	***		n.s.		n.s.
A. albifrons	m>f	**	m>f	*	m>f	***		n.s.	m>f	*		n.s.		n.s.
A. bilineatus	m>f	***	m>f	***	m>f	***		n.s.	m>f	***	f>m	*	m>f	*
A. cinereus	m>f	***	m>f	***	m>f	***	m>f	*		n.s.	f>m	*		n.s.
C. albimacula		n.s.	m>f	**	m>f	*		n.s.		n.s.		n.s.		n.s.
C. annulicornis	m>f	***	m>f	***	m>f	***	m>f	**	m>f	***	m>f	**	m>f	***
C. dissimilis	m>f	***	m>f	***	f>m	***	m>f	*	m>f	***	m>f	***	m>f	***
M. azurea	m>f	**	m>f	***	m>f	***		n.s.	m>f	*	f>m	*		n.s.
M. longicornis		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
M. nigra	f>m	*		n.s.	m>f	***	f>m	***		n.s.	f>m	**	f>m	**
O. lacustris	f>m	***	f>m	**	f>m	*		n.s.	f>m	***	f>m	**	f>m	***
O. notata		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
O. ochracea		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
Odontoceridae														
O. albicorne	f>m	**	f>m	*		n.s.	f>m	**		n.s.	f>m	***	f>m	***
Philopotamidae														
C. trimaculatus	f>m	***	f>m	***	f>m	***	f>m	***		n.s.		n.s.		n.s.
P. ludificatus	f>m	***	f>m	***	f>m	***	f>m	***		n.s.	f>m	*	f>m	*
P. montanus	f>m	***	f>m	***	f>m	***		n.s.	f>m	***	f>m	***	f>m	***
W. occipitalis		n.s.		n.s.		n.s.	f>m	*	m>f	*		n.s.		n.s.
Polycentropodidae														
P. conspersa		n.s.	f>m	**	f>m	***	f>m	**	m>f	*		n.s.	m>f	**
P. flavomaculatus	f>m	***	f>m	***	f>m	***	f>m	***	f>m	***	f>m	*		n.s.
P. irroratus	f>m	**	f>m	***	f>m	***		n.s.		n.s.		n.s.		n.s.
Psychomyiidae														
L. phaeopa	f>m	***	f>m	***	f>m	**	f>m	**		n.s.	f>m	**	f>m	*
L. reducta	f>m	***	f>m	***		n.s.	m>f	***	f>m	***	f>m	***	f>m	***
P. pusilla	f>m	***	f>m	**		n.s.	f>m	***		n.s.	f>m	***	f>m	**
T. waeneri		n.s.		n.s.	f>m	*		n.s.	m>f	*		n.s.		n.s.
Rhyacophilidae														
R. dorsalis		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
R. fasciata		n.s.		n.s.		n.s.		n.s.		n.s.	m>f	*	m>f	*
R. nubila	f>m	**	f>m	***	f>m	***	f>m	***		n.s.		n.s.		n.s.
R. obliterata	m>f	***	m>f	***	m>f	***	m>f	*	m>f	***	f>m	***	f>m	***
R. praemorsa	m>f	***	m>f	**	m>f	***		n.s.	m>f	**		n.s.		n.s.
R. tristis	f>m	**		n.s.		n.s.	f>m	***		n.s.	f>m	***	f>m	***
Sericostomatidae														
O. monedula	f>m	***	f>m	***	f>m	*	f>m	*	m>f	**		n.s.		n.s.
S. flavicorne	f>m	***	f>m	***	f>m	***		n.s.	f>m	***	f>m	*	f>m	*
S. personatum	f>m	***	f>m	*		n.s.		n.s.	f>m	***	f>m	*	f>m	**

3.3.2 Multivariate analysis of morphometry

Altogether, we investigated 2317 specimens representing 1161 male and 1144 female caddisflies belonging to 86 species and 42 genera of the order Trichoptera. The biometric database included now as well the biometric information on Limnephilidae as given in Chapter 1. In the family Limnephilidae we investigated 685 individuals representing 341 male and 344 female adult caddisflies belonging to 26 species and 13 genera.

Principal component analysis, applied to all the morphometric variables, showed that the first principal component (PC1) accounts for 88.37% of total variance, whereas the second principal component (PC2) accounts for 7.35 % of the total variance, cumulatively explaining 95.72 % of total variance. Through the PCA the data is separated into two major groups: one group consists mostly of limnephilid-species, but also encounters few species-sex groups belonging to Leptoceridae and Psychomyiidae, whereas the second group encompassed 13 of the 14 families tested (Fig. 3.2). The parameters wing length, wing area, body length, and wing with explain the distribution of the limnephilid-species very well, whereas in all the remaining species the RWL does influence the distribution as well (Fig. 3.2). Surprisingly, the aerodynamic indices AR I and II are negligible in explaining the variation of the data (Fig. 3.2).

Different overlays are added to the PCA plot in Fig. 3.2 area displaying species-specific morphological, ecological, sexual or behavioural information.

First, we used the split RWA as an overlay for the data displayed; Fig. 3.3 shows three groups (small, medium, high) which string along the gradient of the morphometric parameters (wing length, wing width, body length and wing area), but is uninfluenced by RWL and the aerodynamic indices.

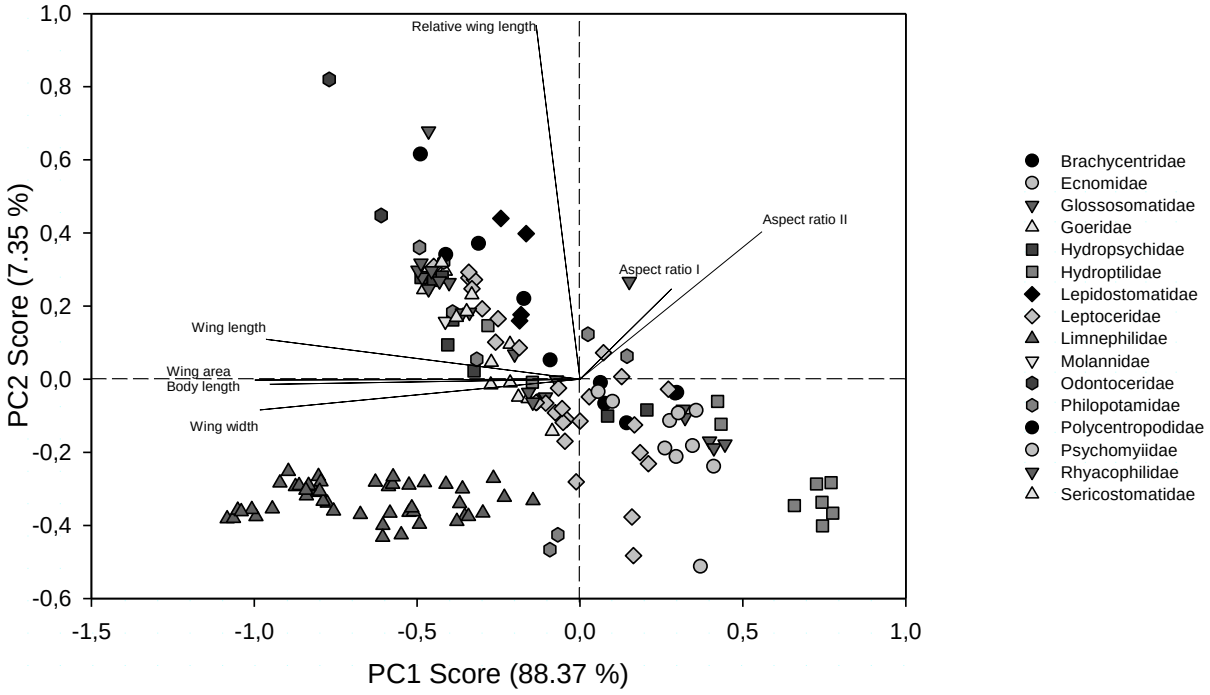

Fig. 3.2: Multidimensional morphometric variation in adult Trichoptera including taxonomic information, illustrated by Principal Components Analysis.

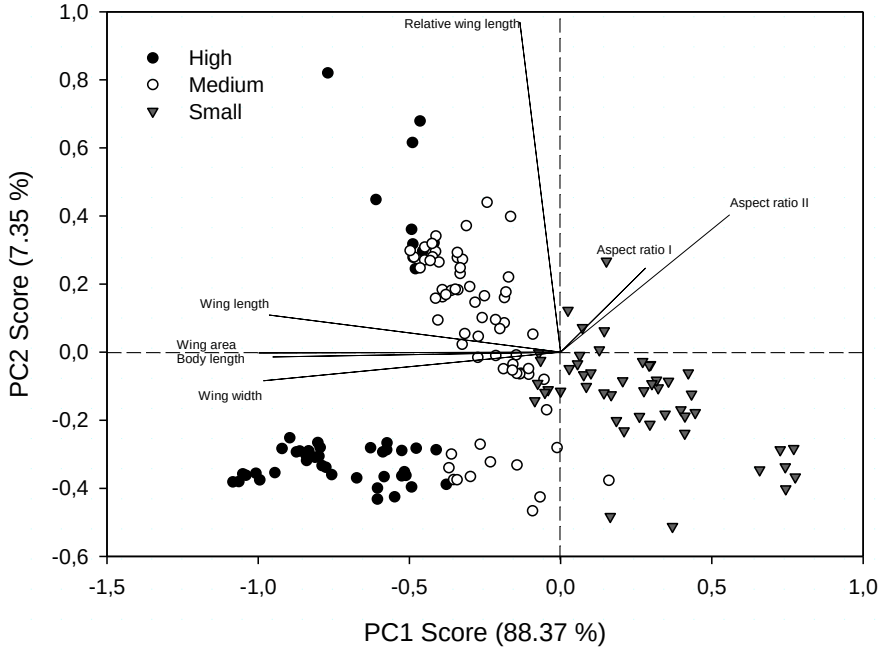

Fig. 3.3: Multidimensional morphometric variation in adult Trichoptera including information on RWA (RWA): High=upper third of RWA, Medium=medium third of RWA, small=lower third of RWA; illustrated by Principal Components Analysis.

Second, we overlayed information on the current regime preferred by the larvae: the morphometric group including the Limnephilidae prefers a lotic regime, whereas the second group shows no distinct preference for either current regime or has no preference at all (Fig. 3.4).

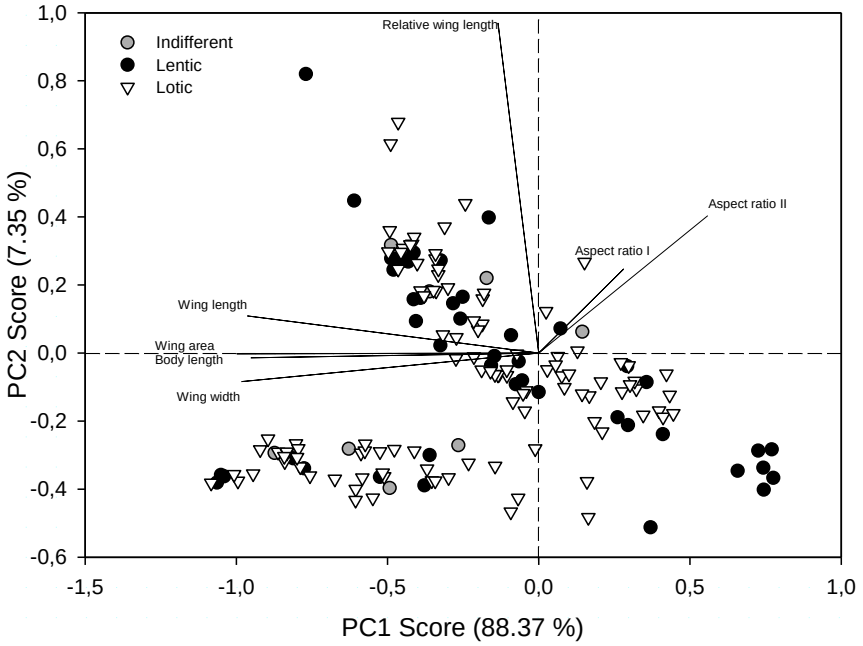

Fig. 3.4: Multidimensional morphometric variation in adult Trichoptera including information on current regime preference: lentic=standing water bodies, lotic=running water bodies, indifferent=no distinct preferences; illustrated by Principal Components Analysis.

Then, we applied the shape for duration of the emergence period (long, short) to the plot; the majority of species investigated have a long emergence period and this is evenly spread over the morphometric variation, but the limnephilid-group has a high amount of species with a short emergence period (Fig. 3.5).

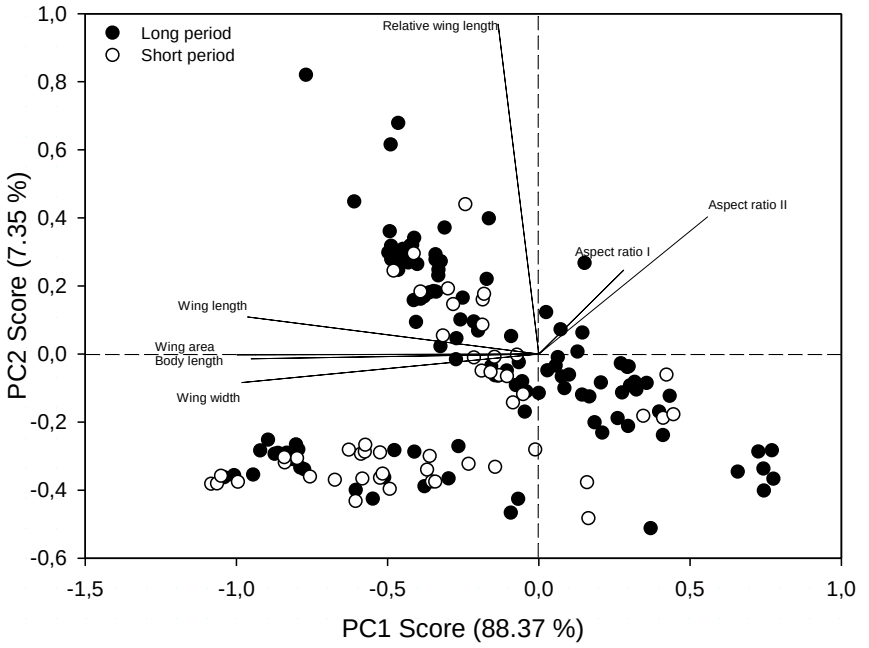

Fig. 3.5: Multidimensional morphometric variation in adult Trichoptera including information on the duration of the emergence period, illustrated by Principal Components Analysis.

Additionally to the t-test on sexual dimorphism we constructed an overlay giving information on the sex of the group tested; in general the distribution is quite balanced (Fig. 3.6).

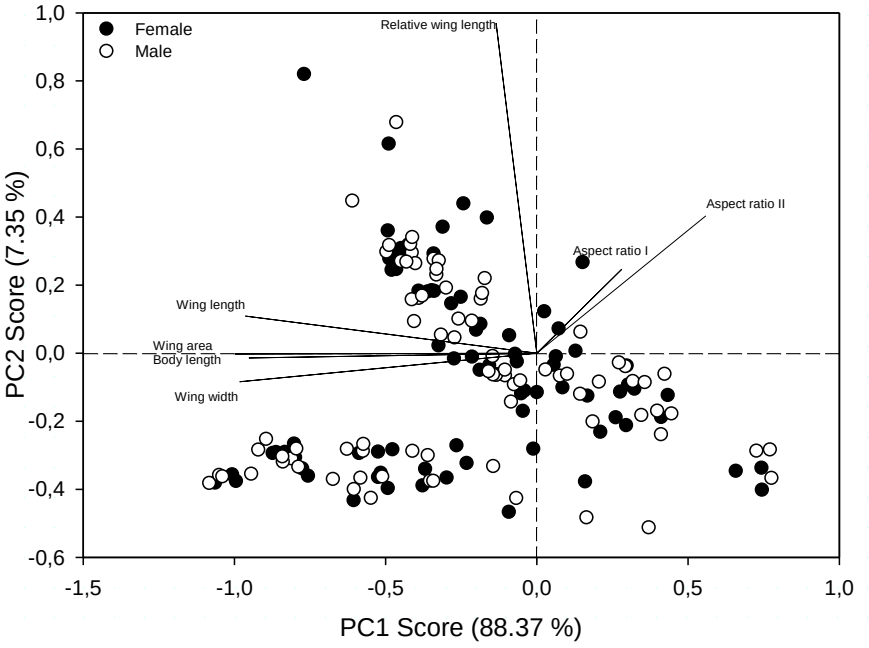

Fig. 3.6: Multidimensional morphometric variation in adult Trichoptera including information on the sex, illustrated by Principal Components Analysis.

Last, we summed the information available on flight behaviour (swarming, not swarming, night active; Tab. 3.6) and night activity as supplement for “not swarming” in an overlay; swarming behaviour seems to be coupled to the medium-RWA group (Fig. 3.7).

Tab. 3.6: Information available on swarming behaviour and activity pattern in adult Trichoptera to the date, expanded due to personal communication.

Species	Swarming behaviour	Reference	Species	Swarming behaviour	Reference
Brachycentridae			Limnephilidae		
M. longulum	not swarming	Graf pers. comm.	*A. auricollis*	swarming	Graf pers. comm.
M. setiferum	not swarming	Graf pers. comm.	*A. nervosa*	not swarming	Graf pers. comm.
Ecnomidae			*A. obscurata*	not swarming	Graf pers. comm.
E. tenellus	not swarming	Graf pers. comm.	*C. villosa*	swarming	Andersen & Tysse 1984
Glossosomatidae			*D. annulatus*	night active	Graf pers. comm.
A. delicatulus	night active	Ehlert 2009	*D. discolor*	night active	Graf pers. comm.
A. fuscipes	not swarming	Graf pers. comm.	*E. dalecarlica*	night active	Graf pers. comm.
A. ochripes	night active	Ehlert 2009	*E. guttulata*	night active	Graf pers. comm.
G. boltoni	not swarming	Graf pers. comm.	*G. pellucidus*	not swarming	Graf pers. comm.
G. conformis	not swarming	Graf pers. comm.	*H. digitatus*	no information	
Goeridae			*H. radiatus*	no information	
G. pilosa	not swarming	Graf pers. comm.	*L. centralis*	night active	Graf pers. comm.
S. nigricornis	swarming	Ehlert 2009	*L. extricatus*	night active	Graf pers. comm.
S. pallipes	swarming	Ehlert 2009	*L. flavicornis*	night active	Graf pers. comm.
S. piceus	swarming	Ehlert 2009	*L. fuscicornis*	night active	Graf pers. comm.
Hydropsychidae			*L. griseus*	night active	Graf pers. comm.
C. lepida	no information		*L. lunatus*	night active	Graf pers. comm.
H. pellucidula	swarming	Benz 1975	*L. rhombicus*	night active	Graf pers. comm.
H. saxonica	swarming	Gruhl 1960	*L. sparsus*	night active	Graf pers. comm.
H. siltalai	swarming	Andersen & Klubnes 1983	*M. lateralis*	night active	Graf pers. comm.
Hydroptilidae			*P. picicornis*	not swarming	Graf pers. comm.
A. pallicornis	not swarming	Graf pers. comm.	*P. cingulatus*	not swarming	Graf pers. comm.
H. angustipennis	swarming	Hickin 1968	*P. latipennis*	not swarming	Graf pers. comm.
H. forcipata	not swarming	Graf pers. comm.	*P. luctuosus*	not swarming	Graf pers. comm.
H. sparsa	not swarming	Graf pers. comm.	*P. nigricornis*	not swarming	Graf pers. comm.
I. lamellaris	not swarming	Graf pers. comm.	*S. permistus*	not swarming	Graf pers. comm.
Lepidostomatidae			Molannidae		
L. basale	swarming	Ehlert 2009	*M. angustata*	swarming	Solem & Petersson 1987
L. hirtum	night active	Graf pers. comm.	Odontoceridae		
Leptoceridae			*O. albicorne*	night active	Graf pers. comm.
A. reducta	swarming	Graf pers. comm.	Philopotamidae		
A. albifrons	swarming	Gullefors & Petersson 1993	*C. trimaculatus*	swarming	Graf pers. comm.
A. bilineatus	swarming	Gullefors & Petersson 1993	*P. ludificatus*	swarming	Hering 1992
A. cinereus	swarming	Gullefors & Petersson 1993	*P. montanus*	swarming	Hering 1992
C. albimacula	swarming	Gullefors & Petersson 1993	*W. occipitalis*	swarming	Graf pers. comm.
C. annulicornis	swarming	Gullefors & Petersson 1993	Polycentropodidae		
C. dissimilis	swarming	Gullefors & Petersson 1993	*P. conspersa*	night active	Müller 1973
C. fulva	swarming	Gullefors & Petersson 1993	*P. flavomaculatus*	swarming	Solem 1980
C. nigronervosa	swarming	Gullefors & Petersson 1993	*P. irroratus*	swarming	Solem 1980
M. azurea	swarming	Gullefors & Petersson 1993	Psychomyiidae		
M. longicornis	swarming	Gullefors & Petersson 1993	*L. phaeopa*	swarming	Graf pers. comm.
M. nigra	swarming	Gullefors & Petersson 1993	*L. reducta*	swarming	Graf pers. comm.
O. lacustris	swarming	Gullefors & Petersson 1993	*P. pusilla*	not swarming	Botosaneanu 1957 in Ehlert 2009
O. monedula	no information		*T. waeneri*	not swarming	Graf pers. comm.
O. notata	swarming	Gullefors & Petersson 1993	Rhyacophilidae		
O. ochracea	swarming	Gullefors & Petersson 1993	*R. dorsalis*	not swarming	Graf pers. comm.
			R. fasciata	not swarming	Graf pers. comm.
			R. nubila	night active	Ehlert 2009
			R. obliterata	not swarming	Graf pers. comm.
			R. praemorsa	not swarming	Graf pers. comm.
			R. tristis	swarming	Graf pers. comm.
			Sericostomatidae		
			S. flavicorne	not swarming	Ehlert 2009
			S. personatum	not swarming	Ehlert 2009

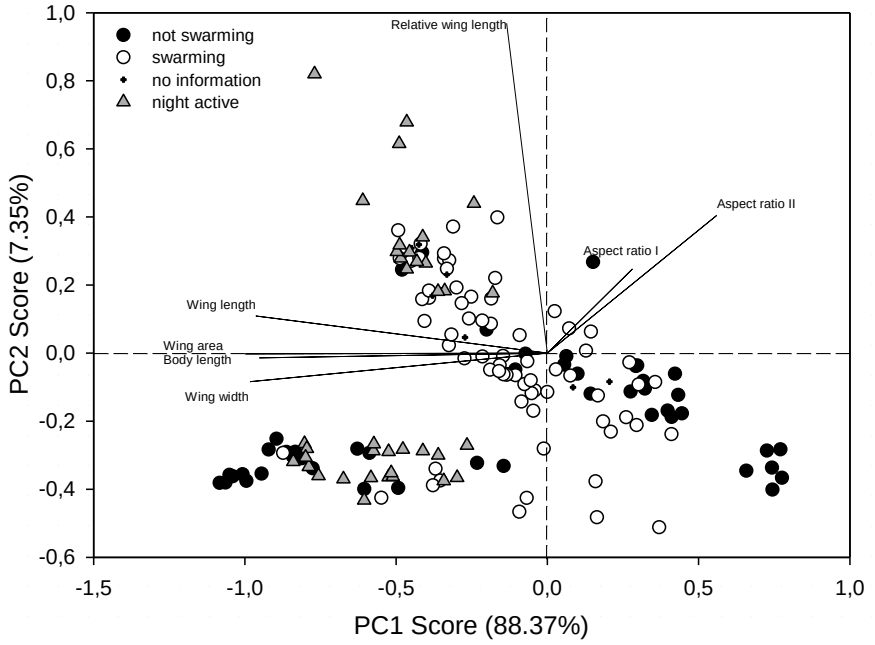

Fig. 3.7: Multidimensional morphometric variation in adult Trichoptera including information on the flight behaviour (not swarming, swarming, no information) and night activity, illustrated by Principal Components Analysis.

In general, species resembling the morphometry of the Limnephilidae are different from other species in many other aspects too, as emergence period, current preference, and flight behaviour.

3.4 Discussion

We acquired a very detailed species-sex specific flight-morphology database and tested for possible morphological blueprints. On genus-level most blueprints are similar supporting the current taxonomy. Apart from most genera, we found a high variability in morphometry in *Hydropsyche*, *Athripsodes*, *Ceraclea*, *Oecetis*, and *Rhyacophila*. All the wing lengths measured are in the range given by Malicky (2004). Hoffsten (2004) collected species-sex specific biometric data in Swedish caddisflies; in *Lepidostoma*, *Polycentropus*, and *Sericostoma* biometric values are comparable to ours, but our females of *M. azurea* and *P. irrotatus* are bigger.

Gullefors & Petersson (1993) investigated the morphology of northern Leptocerid caddisflies and discovered a relation between male-to-female wing ratio and pair formation patterns. We compared our data with the data given by Gullefors & Petersson (1993) and found that our

values are lower in *Ceraclea* and higher in *Oecetis*. Reasons for this discrepancy might be the different provenance of material and the high number of individuals tested by Gullefors & Petersson (1993).

We also evaluated data for all species. Goretti et al. (2005) stated that biometric regression and their equations allow the estimation of the relationships between the linear dimensions of various body parts in the order Trichoptera; they found a high degree of isometry in the order. Hence, we analysed the relationship of wing length to body length (r^2=0.76) in untransformed data; this relationship was not as strong as the relationship (r^2=0.956) detected in ln-transformed data by Goretti et al. (2005) who used the "G. P. Moretti Collection" (University of Perugia). Ln-transformation (r^2=0.72) did not strengthen our relationship. Forewing lengths and wing width show the highest correlation with body length in untransformed data. Consequently, the common use of forewing length for identification of the size of a species in the order Trichoptera (Malicky, 1983; Neboiss, 1986) is justified on the basis of these relationships. Moreover, its use is facilitated by the simplicity of measurement and the fact that the wing remains unaltered by any of the preservation techniques (Goretti et al. 2005). Additionally, we analysed the biometric data with a PCA, on which we applied a hierarchy shape resembling the current taxonomy.

The limnephilid species are well separated from all other species analysed. The following species show the same biometric pattern as the Limnephilidae: *W. occipitalis* (Philopotamidae, both sexes), *A. reducta*, and *C. dissimilis* (Leptoceridae; both sexes and females, respectively), as well as *L. reducta* (Psychomyiidae; males). All other tested species are built on a different biometric blueprint. Therefore we conclude, that our initial thesis, size proportions are specific on some hierarchy level, is supported on the family-level by the PCA plot. Holzenthal et al. (2007) stated that the Limnephilidae are the dominant group in much of the Northern Hemisphere at higher latitudes and elevations. As well they are known for longevity and an adult diapause. All this could contribute to the morphological difference to all other Trichoptera tested.

We took three different approaches to quantify sexual dimorphism in flight-morphology. The male-to-female wing length ratio resembles the size proportion between the forewings of both sexes, but no information on the strength of the relationship is given. The PCA-shape on sexual

dimorphism shows higher dispersion in AR I and II in female flight-morphology, whereas males seem to be less influenced by aerodynamical indices. Hence, we took t-tests on all parameters measured and calculated; in absolute body measures females are bigger in about 50% of the species, in 30 % there is no difference, and in the remaining species males are bigger. In AR I and II females are the suggested dispersers in most species (50 % and 30 %), in a large number of species is no difference (40% and 50%) and in a few species only males are the suggested dispersers (10% and 15%, respectively). Our initial hypothesis, that females are the dispersing sex, is supported in most species, if the flight morphology only is considered. Species with dispersing males prefer mostly the rhithral stream zone, but occur from hypocrenal to mesopotamal and littoral. All species except *M. azurea* are bound to some kind of mineralic habitat.

Our third hypothesis was that there is a relationship between the duration of the emergence period (long, short) and the biometry. The information on the duration was compiled to a shape for the PCA plot. The most limnephilid species have a long emergence period but in all other families few species only have a long emergence period. Therefore we conclude that no morphometric pattern is exclusively accounting for a long or short emergence period. Hence, the morphometric pattern of the Limnephilidae suggests long emergence periods, but there is no strict relationship detectable.

Our fourth hypothesis links flight-morphology, function and behaviour. We stated that there is a relationship between the RWA and the mating behaviour of caddisflies. On that account, we applied the value of RWA on one PCA-shape and the available information on swarming behaviour on another. If both shapes are compared, most species with a small to medium sized RWA do swarm, but species with a high RWA value usually do not swarm. Nevertheless, we found no exact relationship between RWA and flight behaviour, but do interpret the result as a link between morphology and behaviour. Small caddisfly species have thin wings, which do not enable them to manoeuvre well. As well the total mass of small species is low. Viscosity of air decreases with the increasing size of the object. Hence, flight is proportionally more energy-consuming for small animals. Very big species are therefore able to fly quite energy efficient if a medium flight velocity is reached because the drag forces are strong at low Reynolds numbers which makes it ‘relatively more difficult to get anywhere’ (Vogel, 1981). Medium sized caddisfly

seem to operate at aerodynamical conditions where the physical environment and conditions (viscosity and drag forces) enable medium velocity flight and swarming.

Finally, we stated that lentic species do have a greater urge to disperse due to a higher risk of disturbance in their larval habitat. Lentic species are seldom found in the Limnephilid group, but lotic species are evenly spread over both morphometric patterns. Consequently, we conclude that lotic species spread their ability to disperse on all possible morphometric patterns, whereas the morphometric pattern of the limnephilid species is seldom associated with a lentic current environment. This implies that the “Limnephilidae-blueprint” does not suit the dispersal needs for lentic species which differ from the needs of lotic species due to the habitat stability in time.

4. Discussion

4.1 Background

The aim of this study was to clarify the flight-ability and dispersal strategies of many Central European Trichoptera species and to circumstantiate the stated hypothesises.

First, we stated that flight morphology in itself shows strong linear relationships on various taxonomic levels. We found relationships between forewing length and body length on all levels tested. In the Limnephilidae the relationship was strong ($r^2 = 0.88$), as well as in the whole data-set ($r^2 = 0.78$), but in the Goeridae it was not especially strong ($r^2 = 0.52$). Additionally, we calculated the regression sex-specific for the Goeridae: in the females the regression is strong ($r^2 = 0.83$), but in the males is barely existent ($r^2 = 0.06$). Therefore, we conclude that the variation within one genus is higher than within one family. If the whole data-set is considered the relationship reaches only medium strength. This contradicts Goretti et al. (2005) who stated that all Trichoptera follow one blueprint.

Our second hypothesis was that sexual dimorphism in morphology favours females as dispersing sex and that this reflects in dispersal morphology. On the species level this is supported in most species considered, but not in all. On the genus level we find different patterns. In most genera females only are the dispersing sex (Glossosomatidae: *Agapetus*, Polyenctropidae: *Polycentropus*), if morphology only is considered. In some genera it is only the males whom are suggested by morphology to disperse (Leptocerdiae: *Athripsodes*, Limnephilidae: *Limnephilus*). In three genera the morphology gives no indication for the whole genus, but changes from species to species (Goeridae: *Silo*, Hydropsychidae: *Hydropsyche* and Rhyacophilidae: *Rhyacophila*).Hence, the hypothesis is not entirely supported and the picture is more complex than initially anticipated. This is also stated by contradictory observations documented in the literature. Although little information is available on flight behaviour of male limnephilid caddisflies, females in different stages of reproductive development (immature, gravid and spent) in a Swedish stream exhibit non-random inland distribution (Svensson, 1974).

Then we investigated, if wing morphology reflects the ecological preferences species based on the hypothesis that ecological generalists will disperse more frequently as the danger of landing in an unsuitable habitat is low. In the Limnephilidae we find a low-dispersal morphological blueprint in species with habitat specialism (e.g. *P. picicornis*, *D. discolor*) and a high-dispersal blueprint in species without specialism (e.g. *P. nigricornis*, *P. luctuosus*). These different blueprints sum up species with habitat specialism regardless their taxonomy. The blueprint for specialism encompassed at least two genera depending on the parameter considered. The species comparison did not shed light on the situation as the goerid-species are very similar in their ecological requirements. On the larger scale of analysis we find took emergence period duration as ecological parameter. The two general blueprints ("Limnephilidae-blueprint", "All-blueprint") we find a weighting in emergence period: the "Limnephilidae-blueprint" encompasses evenly long and short emergence periods, but the "All-blueprint" is associated more strongly to a long emergence period. We understand short emergence periods as specialism as the timing for successful survival of the population is stricter. Hence, we conclude that our hypothesis is supported and we identified different blueprints for different ecological strategies.

Last, water bodies differ in their current regime; running waters (lotic) are considered quite stable in time, whereas standing water bodies (lentic) are considered comparably instable, if evolutional time frames are considered. Species inhabiting lentic environment have a greater urge to disperse than lotic species because the risk to lose a whole population is higher. In the Limnephilidae we find a small group of lentic species resembling the same morphological patterns. These species do not belong to only one genus. Considering all species we the "All-blueprint" in species of both current regimes, but the "Limnephilidae-blueprint" is lotic biased. There are very species which are indifferent in current terms. They distribute evenly on both blueprint patterns. Hence, we support the hypothesis that different current regimes are reflected in morphology. Apart from this we have to stress that the morphology pattern resembles mediocre dispersal ability.

4.2 Conclusions and future prospects

As dispersal is a hot topic due to the restoration process of European freshwater ecosystems results on dispersal strategies are valuable for the planning process of restoration projects. Although our results fail to quantify dispersal ranges, we are able to construct a hierarchy of dispersal abilities based on flight morphological features. Species occurring in the crenal and species with habitat specialism have the least capacity to disperse. Morphologically they are followed by the group of species inhabiting a lentic current environment. Generalists and species occurring in the rhithral current regime are morphologically equipped to disperse farther. Generally, we can say that specialism will limit the morphological features for dispersal. The consequence for a successful restoration process must be that the distance between crenal areas should be bridged by breeding habitats for crenal specialist. Lentic species will be able to reach new breeding habitats in farther distance and generalists are morphologically entitled to reach new habitats in even greater distance. Still, we have to take into account that the morphology itself is not dispersing at all. The individual has to use its morphological equipment to get anywhere and not every individual of a population will disperse. Dispersal behaviour will be species-specific as the flight experiment with *Silo* spp. showed impressively. As well, when assessing the ecological status of a restored site the time frame has to be considered. In a given timeline we would expect the generalists to arrive first, followed by lentic and current indifferent species, and the specialist will be last.

Apart from the restoration considerations we find additional general statements on the dispersal of caddisflies. The morphometric results certainly circumstantiate that adult caddisflies have more than one general blueprint. Different evolutional development lines have formed within the caddisflies, separating the Limnephilidae from most other families with only few exceptions. On the genus-scale we find different variation patterns, genera with high variation in morphology (e.g. Leptoceridae: *Ceraclea*) and genera with an affixed blueprint (e.g. Rhyacophilidae: *Rhyacophila*). These results can be interpreted in two ways: high variation occurs due to evolutional development processes or the given taxonomy is not congruent with morphological development. The sampling size used was medium and we are positive, that there are more differences to prove with an enlarged data-set and sample size.

The purpose of the aerodynamic indices is to discriminate different groups of dispersing strategies in Trichoptera. The PCA showed impressively that the explanation values of AR I and

AR II are very low. These aerodynamic indices are frequently used parameters in ornithology and the technological sciences. Hence, we will have to find other measures to quantify and/or discriminate groups of species according to their dispersal capacity.

The mass data acquired in *Silo* enhanced the complexity of the picture. The aim of finding a relationship between flight morphology including mass parameters, fecundity state, and flight distance could not be accomplished since we could not quantify the actual flight performance of *Silo*. Flight experiments proved to be very time and resource consuming. Apart from strict flight experiments, the acquisition of a standardised mass data-set in various fecundity states will cast light on this topic and enable more specific explanations. Without mass parameters and flight distance data the picture is more difficult to analyse, as morphological flight ability consists of two structures, first the actual wings which operate as joined aerofoils and second, the flight muscles which operate the aerofoils. One overall parameter on top of this is the behaviour because a flying caddisfly only will be able to travel far enough to reach new catchments. The mere analysis of wings and wing-morphology gives us a first clue of the flight-equipment design realized within Trichoptera.

Nevertheless, we found a very interesting relationship between morphology and flight behaviour, which should be investigated further.

In order to give more specific answers on dispersal of adult Trichoptera we need additional field studies quantifying distance ranges and vertical migration patterns in caddisfly species. Additionally, genetic studies on neighbouring catchments can define the amount of genetic exchange between adjacent populations. Alongside with the genetic exchange the specimen exchange is documented. Strategies of dispersal in various fecundity states are the acquisition of new habitats with given genetic equipment (fertilised eggs) or the acquisition of a new habitat and genetic material (unfertilised eggs). All of which will have influence on the genetic equipment of a given population. Another interesting aspect is the (re-)immigration of locally extinct species into newly restored habitats. This can be studied in the monitoring of the restoration process of European freshwater systems.

In conclusion, we find very strong relationships within the morphology of adult caddisflies, a “limnephilid-blueprint” and one different blueprint and relationships between morphology,

ecological and behavioural preferences. In the blueprints we find generalists to be equipped with a morphology set designed for dispersal, whereas specialists do come with a non-dispersal morphological equipment. Apart from the morphology other factors influence the actual dispersal distance of one individual or species: muscle mass, behaviour, weather conditions, and topography.

5. Summary and future prospects

5.1 Summary

We addressed current questions in the adult dispersal of Trichoptera:

First, we investigated flight morphological features characterising dispersal ability and tested for relationships within and between species and families.

Second, since literature on sexual dimorphism is contradictory we tested on sexual dimorphism to clarify if we can identify a general dispersing sex.

Last, habitats do differ in their stability in time and standing water bodies are considered comparably instable. We investigated if this instability of habitat is resembled in the morphology.

Summary of the most important results

Chapter 1:

Wing-morphology of selected limnephilid caddisflies (Insecta: Trichoptera: Limnephilidae) in relation to their habitat preferences

- We found strong linear relationships between forewing length and body length (r^2=0.88), wing width (r^2=0.96), and wing area (r^2=0.88) in untransformed data.
- Sexual dimorphism proved to be species-specific. In the directly measured wing parameters males exceed females in all significant species except *P. picicornis*. In the aerodynamic indices only 28 % of species show sexual dimorphism, in *L. fuscicornis* and *P. luctuosus* males exceed females (11%), and in *D. annulatus*, *D. discolor*, and *P. cingulatus* females exceed males (27%).
- We found different morphological blueprints in forewing length and wing width resembling ecological preferences in the species tested. The first group of species encompasses crenal inhabiting species with a distinct habitat preference for mineral habitats. The second group encompasses rhithral species without a distinct habitat preference. The third identified group is small and encompasses species inhabiting a lentic current environment and preferring organic habitats.

Chapter 2: Goeridae

Flight-morphology of four goerid caddisflies (Insecta: Trichoptera: Goeridae) in relation to habitat preferences

- We bred 90 specimen of Silo spp. in lab and 60 individuals emerged successfully.
- We developed a new technique to quantify the flight performance of individuals in the lab. Only one of 60 individuals tested showed a constant, measurable flight performance. The individual reached a medium velocity of 0.124 m s-1 and a total distance of 46.99 m in 765 seconds. The flight was divided into 5 laps.
- We gained species-specific and standardised mass data from the emerged lab individual of *Silo* spp.
- We found a difference in the morphological blueprint between the genera *Goera* and *Silo*.
- The regression analysis showed a strong relationship between forewing length and body length in females of all species (r^2= 0.83), but all remaining relationships calculated were weak to barely existent.
- Sexual dimorphism was present in all species. In *G. pilosa* males exceeded females in directly measured parameters. In *Silo* spp. size parameters were male biased, except forewing length in *S. nigricornis* which was vice-versa. The dimensionless indices were insignificant in *G. pilosa* and male biased in *Silo* spp.
- Sexual dimorphism was present in mass parameter in *S. nigricornis* and *S. pallipes*. In total mass and thorax mass females exceeded males, but in RTM and wing loading the situation was vice-versa.
- We found morphologically similar groups within the dataset. In forewing length species groups formed in species inhabiting a overlapping stream zones, adjacent altitudinal preferences, and similar emergence periods.

Chapter 3: Central European Species

Flight-morphology of German Trichoptera (Insecta) in relation to their ecological preferences and flight behaviour

- We found strong linear relationships between forewing length and body length (r^2=0.76) and wing width (r^2=0.78) in untransformed data.
- We found different family specific patterns of sexual dimorphism in the data set. Generally females are bigger than males. The most prominent exceptions are the families Leptoceridae and Rhyacophilidae where males exceed females in most species. In the remaining families only in the species *H. siltalai* (Hydropsychidae) males exceed females. In the dimensionless indices the picture changes: in the size independent RWL the data set splits into thirds (20 species males bigger, 21 species similar and 19 species females bigger). In the aerodynamic indices the result is clearly female biased.
- Principal components analysis showed two major morphometric groups in the data set. All limnephilid and few additional species belonging to Leptoceridae and Psychomyiidae resemble the “limnephilid-blueprint”. All remaining species resemble a different blueprint. This distribution is explained to 95.7% with axis 1 and axis 2.
- We constructed a few overlays for the PCA plot based on ecological and behavioural data.
- There is a relationship between the limnephilid-blueprint and the lotic regime, whereas the other blueprint shows no distinct preference for a current regime.
- The limnephilid-blueprint shows a high amount of species with a long emergence period. No pattern is visible in sexual dimorphism.
- The limnephilid-blueprint goes along with no known swarming behaviour.
- In general, species resembling the “limnephilid-blueprint” are different from other species in many other aspects too, as emergence period, current preference, and flight behaviour.

5.2 Future prospects

- The results fail to quantify dispersal ranges; we are able to construct a hierarchy of dispersal abilities based on flight morphological features. Consequently, we do need field studies on flight ranges and vertical migration patterns of caddisflies.
- The mass data acquired in *Silo* enhanced the complexity of the picture. The aim of finding a relationship between flight morphology including mass parameters, fecundity state, and flight distance could not be accomplished since we could not quantify the actual flight performance of *Silo*. A new data-set on mass parameters of adult flight morphology will enable us to rank dispersal capacities more precisely.
- The PCA showed impressively that the explanation values of the aerodynamical indices used are very low. These aerodynamic indices are frequently used parameters in ornithology and the technological sciences. Hence, we will have to find other measures to quantify and/or discriminate groups of species according to their dispersal capacity.
- We found a very interesting relationship between morphology and flight behaviour, which should be investigated further. Hence, we need studies on adult flight and mating behaviour.
- Genetic studies on neighbouring catchments can define the amount of genetic exchange between adjacent populations. Alongside with the genetic exchange the specimen exchange is documented. Strategies of dispersal in various fecundity states are the acquisition of new habitats with given genetic equipment (fertilised eggs) or the acquisition of a new habitat and genetic material (unfertilised eggs or males).
- Another interesting aspect is the (re-)immigration of locally extinct species into newly restored habitats. This can be studied in the monitoring of the restoration process of European freshwater systems.

6. Zusammenfassung

6.1 Hintergrund

Wir haben folgende, aktuelle Fragen zur Ausbreitung adulter Trichopteren bearbeitet

Zuerst haben wir die Flugmorphologie untersucht, die die Ausbreitungsfähigkeit charakterisiert und überprüft, ob morphologische Zusammenhänge innerhalb und zwischen Arten und Familien nachweisbar sind.

Zweitens, da die Literatur in Bezug auf Sexualdimorphismus widersprüchlich ist, haben wir überprüft, ob sich ein ausbreitendes Geschlecht über alle taxonomischen Grenzen hinweg feststellen lässt.

Drittens, wir haben getestet, ob es nachweisebare Beziehungen zwischen ökologischen Ansprüchen und morphologischen Bauplänen einzelner Arten gibt.

Letztens, wir haben überprüft, ob sich die Vorhersagbarkeit eines Habitats (See gelten als gut vorhersagbar) in der Morphologie niederschlägt.

Zusammenfassung der wichtigsten Ergebnisse

Kapitel 1:

Flügel-Morphologie ausgewählter Limnephilidae (Insecta: Trichoptera) in Beziehung zu ihren Habitatansprüchen

- Wir haben eine starke, linear Beziehung zwischen der Vorderflügellänge und Körperlänge (r^2=0.88), Flügelbreite (r^2=0.96) und der Flügelfläche (r^2=0.88) in nicht-transformierten Daten nachgewiesen.
- Der morphologische Sexualdimorphismus ist artspezifisch. In den gemessenen Flügelparametern sind Männchen in allen signifikanten Unterschieden größer als Weibchen. Die einzige Ausnahme dazu ist *P. picicornis*. In den aerodynamischen Indices weisen nur 28% der Arten einen Sexualdimorphismus auf. In *L. fuscicornis* und *P. luctuosus* sind die Männchen größer (11%) und in *D. annulatus*, *D. discolor* und *P. cingulatus* sind die Weibchen größer (27%).

- Wir haben einen Zusammenhang zwischen der Vorflügellänge und Flügelbreite und den ökologischen Habitatansprüchen der getesteten Arten gefunden. Die erste Gruppe wird von Arten gebildet, die das Krenal bewohnen und mineralische Habitate bevorzugen. Die zweite Gruppe wird von Arten gebildet, die das Rhitral bevorzugen und keine bestimmten Habitate bewohnen. Die dritte Gruppe ist klein und umfasst Arten die wenig strömende Zonen bewohnen und organische Habitate benötigen.

Kapitel 2: Goeridae

Flügel-Morphologie von vier Goridae-Arten (Insecta: Trichoptera) und ihre Beziehungen zu Habitatansprüchen

- Wir haben 90 Individuen von Silo spp. im Labor gehältert und einen Schlupferfolg bei 60 Individuen erzielt.
- Wir haben eine neue Technik entwickelt, um die Flugleistung einzelner Individuen im Labor festzustellen. Nur eines von 60 getesteten Individuen zeigte eine konstante, messbare Flugleistung. Dieses Tier hat eine mittlere Geschwindigkeit von 0,124 m s^{-1} erreicht und eine Wegstrecke von 46.99 m in 765 s zurückgelegt. Der Flug war in fünf Phasen unterteilt.
- Wir haben standardisiert Massedaten aller im Labor geschlüpften *Silo*-Individuen erhoben.
- Wir haben Unterschiede im Bauplan zwischen *Goera* und *Silo* festgestellt.
- Die Regressionsanalyse zeigte eine starke, linear Beziehung zwischen Vorderflügellänge und Körperlänge bei den Weibchen aller getesteten Arten (r^2 = 0.83), aber in allen anderen errechneten Beziehungen war der Zusammenhang schwach bis beinahe inexistent.
- Sexualdimorphismus war in allen Arten präsent. In *G. pilosa* waren die Männchen in allen direkt gemessen Parametern größer. In den *Silo*-Arten waren die Männchen in allen Größenparameter größer, aber in der Vorderflügellänge von *S. nigricornis* waren die Weibchen größer.
- In den Gewichtsparameter wurde Sexualdimorphismus in *S. nigricornis* und *S. pallipes* nachgewiesen. Die Weibchen hatten größere Gesamt- und Thoraxmasse, aber in der relativen Thoraxmasse und der Tragflächenbelastung war die Situation umgekehrt.

- In dem Datensatz haben wir morphologisch ähnliche Gruppen identifiziert. In der Vorderflügellänge bildete sich eine Gruppe Arten, die überlappende Fließgewässerzonen und benachbarte Höhenstufen bewohnen, wie auch ähnliche Emergenzperioden haben.

Kapitel 3: mitteleuropäische Arten

Flug-Morphologie mitteleuropäischer Köcherfliegen (Trichoptera: Insecta) und ihre Beziehung zu Flugverhalten und ökologischen Ansprüchen

- Wir haben starke, lineare Beziehungen zwischen Vorderflügellänge und Köcherlänge ($r^2 = 0.76$) und Flügelbreite ($r^2 = 0.78$) gefunden (nicht-transformierte Daten).
- Sexualdimorphismus ist in den Familien unterschiedlich. Im Allgemeinen sind die Weibchen größer als die Männchen. Die größte Ausnahme hierzu sind die Familien Leptoceridae und Rhyacophilidae; hier sind die Männchen in den meisten Arten größer als die Weibchen. In den verbleibenden Familien gibt es nur die Art *H. siltalai* (Hydropsychidae), wo die Männchen größer sind. In den dimensionslosen Indices jedoch sieht das Bild anders aus: die größenunabhängig relative Flügellänge teilt sich in drei Gruppen auf (bei 20 Arten sind die Männchen größer, bei 21 Arten gibt es keinen Unterschied und bei 19 Arten sind die Weibchen größer).
- In der Hauptkomponentenanalyse haben sich zwei morphometrische Gruppe gebildet. All Limnephilidae-Arten und wenige zusätzliche Arten aus den Leptoceridae und Psychomyiidae bilden einen morphologischen „Limnephilidae-Bauplan“. Alle verbleibenden Arten bilden eine weiteren „Alle-Bauplan“. Die Verteilung der Arten wird zu 95.7 % durch die Achse 1 und Achse 2 erklärt.
- Aus bekannten ökologischen und Verhaltensdaten haben wir mehrere Schablonen für die Hauptkomponentenanalyse konstruiert.
- Der „Limnephilidae-Bauplan“ geht sehr häufig mit fließenden Gewässern einher, während wir für den „Alle-Bauplan“ keine Präferenz für bestimmte Strömungsverhältnisse gefunden haben.
- Der „Limnephilidae-Bauplan“ geht sehr häufig mit einer langen Emergenzdauer einher.
- Wir haben keinen Zusammenhang zwischen den Bauplänen und Sexualdimorphismus gefunden.

- Der „Limnephilidae-Bauplan“ geht nicht mit einem bestimmten Flugverhalten einher.
- Zusammenfassend kann man feststellen, da Arten, die dem „Limnephilidae-Bauplan“ entsprechend auch in vielen anderen Aspekten unterschiedlich sind, wie z.B. Emergenzdauer, Strömungspräferenz und Flugverhalten.

6.2 Ausblick

- Eine Quantifizierung von Ausbreitungsdistanzen ist aufgrund der Ergebnisse nicht möglich. Es konnte eine Rangfolge unterschiedlichen Ausbreitungsvermögens festgelegt werden aufgrund der erhobenen, morphologischen Gegebenheiten. Aus diesem Grund wären weitere Feld-Untersuchungen zu Ausbreitungsdistanzen und vertikalen Wanderungen interessant.
- Die erhobenen Masseparameter von *Silo* haben das Bild komplexer werden lassen. Unser Ziel eine Beziehung zwischen Flug-Morphologie inklusiver der Masseparameter, des Fertilitätszustandes und der Flugdistanz herzustellen konnte nicht erreicht werden, da die Flugexperimente mit *Silo* gescheitert sind. Ein zusätzlicher Masseparameter-Datensatz würde es uns ermöglichen die Rangfolge der Ausbreitungskapazitäten genauer festzulegen.
- Die Hauptkomponentenanalyse hat eindrucksvoll gezeigt, dass die Erklärungsanteile der aerodynamischen Indizes sehr gering sind. Diese Indizes werden häufig in der Ornithologie und in der Luftfahrttechnik verwendet. Wir müssen daher andere Maße finden, um zuverlässig morphologische Ausbreitungskapazitäten zu quantifizieren und Gruppen unterschiedlicher Ausbreitungsstrategien bilden zu können.
- Wir haben eine sehr interessante Verbindung zwischen Morphologie und Flugverhalten gefunden, die weiter untersucht werden sollte. Daher brauchen wir weitere Studien zu adultem Flug- und Paarungsverhalten.
- Genetische Untersuchungen von Populationen benachbarter Einzugsgebiete können das Ausmaß an genetischen Austausch quantifizieren. Damit einhergehend kann der Individuenaustausch quantifiziert werden. Strategien der Ausbreitung in unterschiedlichen Fertilitätsstadien sind das erschließen neuer Habitate mit einem vorhandenen Genpool (befruchtete Eier) oder aber die Erschließung eines neuen Habitats und eines neuen Genpools (unbefruchtete Eier oder Männchen).

- Ein weiterer sehr interessanter Aspekt ist die (Wieder-)Einwanderung von lokal ausgestorbenen Arten in neu renaturierte Habitate. Dies ist hervorragend zu untersuchen anhand der Renaturierungsinitiativen in europäischen Gewässersystemen.

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Appendix

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Curriculum Vitae

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten

Erklärung:

Hiermit erkläre ich, gem. § 6 Abs. 2, Nr. 7 der Promotionsordnung der Math.-Nat.-Fachbereiche zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema „*Flight-morphology of Central European caddisflies (Insecta: Trichoptera) in relation to their ecological preferences*“ zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von *Elisabeth H. Müller-Peddinghaus* befürworte.

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